Spatial and temporal patterns in the macroinvertebrate communities in streams

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SPATIAL AND TEMPORAL PATTERNS IN THE MACROINVERTEBRATE COMMUNITIES IN STREAMS.

by

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ABSTRACT

My research looked for evidence of community persistence in two suites of sites. Twenty-nine stream sites were in the Ashdown Forest of southern England and twelve streams which form part of the United Kingdom Acid Waters Monitoring Network. Benthic macroinvertebrates were collected using different methods and the species and physico-chemical data analysed. The Ashdown sites were sampled in 1989 and 1990, and the data collected was compared with previous studies and an analysis made of community persistence over a period of thirteen years. Persistence was assessed using measures of similarity and rank correlation coefficients. The data showed that several physico-chemical factors, in particular stream pH, were related to the structure of the benthic communities. Summer temperatures and stream discharge were also significantly associated with the patterns obtained. Using multivariate methods, TWINSPAN, DECORANA and CANOCO, spatial patterns were discerned. Comparisons of the two previous surveys and my own data showed that sites with low pH, low summer temperatures and low discharge had consistent spatial patterns.

The United Kingdom Acid Waters Network stream sites were originally chosen for their susceptibility to acidification and are located in different geological and geographical parts of the UK. The same persistence measures were used as for the Ashdown data and, although there was greater variability, similar underlying patterns were found. Using the same methods the Ashdown and UKAWMN sites were then analysed together.

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Significance of statistical analyses shown on figures:

*	$0.05 \geq p \geq 0.01$.
**	$0.01 \geq p \geq 0.001$.
***	$p < 0.001$.

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CHAPTER 1.

GENERAL INTRODUCTION.

1.i. Past and present views on stability.

Community ecology is concerned with the description and explanation of patterns in multi-species assemblages. For example, in many groups there are trends in diversity across biomes with latitude, and it has been noted that fewer species are found in the Arctic than in the boreal forests further south. Moving even further south, toward the tropics, it was evident that diversity increased still more (the so called tropical high diversity concept). It was argued by Elton (1958) that, from the patterns emerging, diversity should increase stability. Communities that had a greater number of energy pathways within the system would be less likely to experience large density changes when undergoing perturbations . In the late 1950s' Elton and MacArthur concurred that 'stability' should depend on complexity (complexity relating here to number of species, degree of connectance through the food web, relative abundance etc.). MacArthur's (1955) paper, "Fluctuations of animal populations, and a measure of community stability" and Elton's book "The Ecology of Invasion by Animals and Plants" (1958), contain arguments about stability, what determines it and why its study is important. Elton made the assertion that simple communities are less stable than complex ones, citing evidence from simple predator prey models and simple laboratory experiments such as those done by Gause (1934), and from pest outbreaks within monocultures. While it was certainly true that early simple models and experiments with two-species interactions were often unstable, there was no way of knowing if more complex systems would be any more stable. Nevertheless, at this time the conventional wisdom was that complexity led to stability. Robert May (unpublished) has disparagingly called this idea part of the "folk wisdom" of ecology.

In November 1970, Gardiner & Ashby gave a short paper which, although it recognised that systems may be highly non-linear, as a first step looked at very simple linear systems. As computer modellers, they found that the more components in the model, and the greater the model's connectance, the *less* likely the model is to be stable. Therefore, simple systems were more likely to be stable than complex ones. May (1974) directly tackled the issue of stability in multispecies communities. Essentially, the idea was that the exact patterns of species interactions had substantial impact on whether a model was stable or not. However, even if complexity and instability are related, it does not mean that this holds true for real communities which, unlike models, are not always randomly constructed. A third view has emerged that suggests that if the modellers, empiricists and field biologists were in disagreement, then perhaps they were looking at different parts of a large and complicated field.

The concept of stability is a complex one and when ecologists talk about stability they may be referring to different things. Studying a number of species together poses problems which do not exist in single species studies. Because the term stability is fuzzy in its definition, ecologists are generally studying different aspects of stability - such as resistance, resilience and persistence. In general, the following definitions are accepted, (given by Pimm in 1991). A system is stable only in the mathematical sense if, and only if, the variables all return to equilibrium conditions after displacement from them. By definition, either a system is stable or it is not. The term resistance is used to measure the consequences when a variable is permanently changed. The question is, how much do other variables change as a consequence? If the subsequent changes are small, the system is relatively resistant. Resistance can be said to be measured as a ratio of a variable before and after change, and so is dimensionless.

Resilience is commonly defined as how fast a variable that has been displaced from equilibrium returns to it. Resilience, then, can be estimated by a return time, the amount of time taken for the displacement to decay to some specified fraction of its initial value. Long return times relate to low resilience, and the converse is that short return times correlate with high resilience. Resilience can, therefore, be measured as a rate of change.

The concept of persistence is defined as how long a variable lasts before it is changed to a new value. Systems that often change could be described as having a high turnover, so turnover would be the reciprocal of persistence. Persistence is measured as time. Here we have various meanings of stability which are, in essence, summary statistics which enable us to describe long term patterns.

An ecological system becoming unstable is such a dramatic event it is hard to remember that stability is a relative matter. Over geological time a flood is relatively insignificant. Stability comes from the observer's specification of the system as much as it comes from the system under observation. Like complexity, instability is not a property of the system itself, but an aspect of the mode of the system description. For example, a tree crashing to the forest floor can be seen as the local tree exhibiting instability or as a normal, healthy process of replacement on the forest landscape. One outcome of these discussions on stability has been that it would be unwise to make generalisations for all communities, as so called stable communities may not persist under particular environmental conditions. Some communities, experiencing few perturbations within their predictable environment, could be said to be fragile but stable. Others experiencing large, unpredictable environmental variations would need to be dynamically robust to persist. Here we have additional terminology, 'fragile' and 'robust', and a requirement that the term 'predictability' be defined, not an easy task.

A number of studies have looked at ways of investigating the importance of stability on community structure. Much of this work has been with food webs, (McNaughton 1978; Rejmanek & Stary 1979; Briand 1983; Pimm 1991), who focused very much on the degree of connectance. In addition to the work on food webs, Wolda (1978) concluded that, in general, insect populations from the tropics and from temperate regions have similar annual variability. It very much depends on the scale at which one investigates. There is a large literature on diversity and stability, but little in the way of empirical data to support the many hypotheses. An exception is the work of Van Voris *et* *al* (1980). They used microcosm ecosystems (plugs of soil and vegetation), to test complexity against stability. They did this by looking at the patterns of carbon dioxide released from the microcosms. Each microcosm was ranked according to the number of peaks in their power spectra, (which indicate periodic cycles in the carbon dioxide measurements) with those with the largest number being the most resilient and resistant to disturbance.

1.ii. Freshwater communities.

With regard to aquatic ecosystems, there have been two main hypotheses as to how freshwater communities are structured, reflecting the wider ecological debate. MacArthur (1960) and Cody & Diamond (1975) take the view that species assemblages are systems in equilibrium, mainly structured by biotic and deterministic processes, such as competition. In contrast, Connor & Simberloff (1979) and Strong *et al* (1984) contend that physical and stochastic factors have the greatest influence on community structure. Early studies on the benthos of streams were generally descriptive, linking species distributions with physical or chemical environmental factors (e.g. Hynes 1970). The late 1970's and 1980's have seen an increase in experimental work. Evidence for competition for space (McAuliffe 1983; Peckarsky & Penton 1990), and predation, (Schofield 1988, Lancaster 1990; Lancaster, Hildrew & Townsend 1991) has been forthcoming, although how these local interactions among individuals influence the community as a whole, and at larger spatio-temporal scales, is still being debated, (e.g. Hildrew & Giller 1994).

Vannote *et al's* "river continuum concept" (1980), suggested that there were environmental gradients along the length of a river which are associated with changes in community structure.The continuum concept clearly sees lotic communities as equilibrial, and with a strong role for resource limitation and resource partitioning among species. Influential as it has been, many river ecologists clearly disagree with this view (Winterbourn *et al* 1981; Statzner & Higler 1986; Townsend 1989).

Another approach to lotic communities, ideologically neutral as to the role of species interactions, has been to attempt to classify river systems. Multivariate techniques of ordination and classification have been used to produce objective groupings of stream sites based on their species composition (Townsend *et al* 1983; Wright *et al* 1984; Ormerod & Edwards 1987). The patterns produced by these groupings can then be related to environmental data using correlation and multiple discriminant analysis. A further advance, using canonical analysis, allows for species by sites to be analysed along with the environmental data.

1.iii. Acid waters.

There has been increasing concern over the effects of acid deposition on freshwater systems (Okland & Okland 1986; United Kingdom Acid Waters Review Group 1988), especially in upland areas. Particularly at risk are regions with solid geology and soils with a poor buffering capacity, with afforested catchments being particularly sensitive (Harriman & Morrison 1982; Stoner *et al* 1984). There are also some areas which are naturally acid, even in the absence of acidic depositions (Collier & Winterbourn 1987).

As reported by Townsend *et al* (1987), the acid to circumneutral streams of the Ashdown Forest in south-east England showed variable persistence in their benthic invertebrate communities. Using a variety of statistical methods they illustrated that, over time, these communities generally appeared to be relatively stable. The macroinvertebrate fauna of acid streams is known to be impoverished in species, generally containing half the number of taxa found in circumneutral sites, and the streams are generally unproductive (Townsend *et al* 1983; Hildrew *et al* 1984; Burton & Allen 1985; Otto & Svenson 1983; Ormerod & Edwards, 1987)

Certain animals are almost always absent, these include the amphipod *Gammarus pulex*, which is not found in waters with a pH below 5.7 (Sutcliffe 1972; Sutcliffe & Carrick 1973), and a number of mayfly species, including those in the genus *Baetis*. Although acid sensitive species are also absent from acid lakes, surveys of them have found that these sites are often species rich, suggesting that other species may exploit vacant niches (Okland & Okland, 1986).

The impoverished nature of acid systems appears to reflect the physiological intolerance of many species. This includes disruption of osmoregulation and the consequences of increased concentrations of toxic metals, particularly aluminium (Hall *et al* 1988; Burton & Allen 1986). In addition, there may be indirect effects, such as a reduction in productivity, that are passed up the food chain. This so called "bottom up" hypothesis envisages a depleted or poor quality food resource. Evidence of poor quality food resources in acid streams comes from work by MacKay & Kersey (1985) and Groom & Hildrew (1989), where it has been shown that leaf litter from low pH streams has a reduced rate of microbial decomposition. In addition, the epilithon on the surface of stones was shown to be of poorer quality than that of circumneutral stream sites (Winterbourn *et al* 1985). Work by Sutcliffe & Carrick (1973), showed that in the acid streams they examined, herbivorous macroinvertebrates were absent. In the Ashdown Forest, Townsend *et al* (1983) also found a reduced number of grazer/scrapers. In acid stream sites, where predators are affected by acidification, a "top down" hypothesis may also operate.The effects of predation on community structure is fairly well documented for freshwater systems. Acid lakes with no predatory fish have a plankton made up of large bodied species (Zaret 1980) and, in streams, the absence of brown trout may permit high densities of large predatory insects (Schofield 1988).

1.iv. Persistent communities.

Communities are considered to be resistant if the component organisms are particularly adapted to the physical and chemical environment, tolerate the conditions and thus are able to persist unchanged through disturbances such as pollution or flow events. They are resilient if they exhibit an ability to bounce back after such an event. As previously mentioned, persistence is measured over time, and there are relatively few studies which have looked at aquatic communities over long periods of time. There are two main approaches to studying community persistence, that may be referred to as the "snapshot" and the "trajectory" approaches. The first looks at a large number of sites on a few occasions and the second looks at one or a few streams on a regular basis over a number of years. Both methods have their drawbacks, the snapshot giving too few replicates in time and the trajectory too few replicates in space.

In the Ashdown Forest in south-east England, a relatively large number of streams were sampled in 1976 by Townsend *et al* (1983). A number of these sites were naturally acidic and, using multivariate ordination and classification, it was found that community structure was strongly related to the variation in mean site pH, with summer temperature and discharge also playing significant roles. In 1984 there was a second survey of twenty-seven of the original thirty-four stream sites, to investigate community persistence. It was found that species assemblages at upstream, acidic sites were more persistent than those further downstream, and it was suggested that these were sites experiencing little environmental change - and they might, therefore, be influenced by deterministic processes, whereas stochastic influences might be greater in the sites whose physicochemistry was less predictable. These two studies have given us a database of information to which we can add. In 1989 and 1990 I surveyed the same sites and have, therefore, increased the timescale to thirteen years. The number of sites used for comparison over all three sampling occasions was twenty-six.

In addition, we have been fortunate that the freshwater laboratory at Queen Mary and Westfield College, University of London has been contracted to carry out the invertebrate sampling for the United Kingdom Acid Waters Monitoring Network (UKAWMN) in lakes and streams throughout the United Kingdom. The survey takes place annually (for a minimum period of ten years), and began in 1988. It was established to provide long term high quality biological and chemical data to facilitate the assessment of trends in surface water acidity in the UK. This has given me the opportunity to look for evidence of community persistence in another suite of sites, separated from those in the Ashdown Forest by geology and geography.

For this research I have undertaken to survey both the Ashdown Forest and the UKAWMN suite of sites. My objectives have been to look for evidence of community change or persistence. Rigorous evidence of the temporal changes in natural communities is important in the interpretation of monitoring programmes. If communities are normally invariant from year to year, then detection of a change during monitoring is easy both to detect and to ascribe to environmental change. If, on the other hand, communities are highly variable, even in the absence of sustained environmental change, then community responses will be much more difficult to detect and to interpret.

By using the same methods as were utilised by Townsend *et al* (1987), it has been possible to calculate similarity indices to measure the extent to which species remained in common at a site between years. With rank correlation coefficients between species abundances at each site, we can assess changes in relative abundances over time, and multivariate ordination and classification can be used to assess changes in ordination space. Canonical analysis, using the program CANOCO, is a new method of multivariate analysis, in effect an enhancement of ordination techniques such as DECORANA (DEtrended CORrespondance ANAlysis). CANOCO allows for the ordination together in low dimensional space of species, sites and environmental variables.

Using these methods I have specifically endeavoured:

i) to look for evidence that the spatial patterns revealed in earlier surveys in the Ashdown Forest sites were robust.

ii) to see if the pattern of persistence among sites revealed by Townsend *et al* (1987) were repeated.

iii) to examine the UKAWMN suite of stream sites to characterise their persistence over time.

iv) to relate the structure of these communities, and their persistence, to pH and other environmental variables and to compare the two suites of stream sites.

v) to assess two sampling methods used in the two surveys for comparability.

CHAPTER 2.

SITE DESCRIPTIONS.

2.i. INTRODUCTION.

Two suites of sites have been examined in this study. The first consists of twenty-nine stream stations in the Ashdown Forest, in southern England, and the second the twelve streams from the United Kingdom Acid Waters Monitoring Network. The Ashdown Forest suite of sites consists of both acid and circumneutral streams while the UKAWMN stream sites, chosen for the purpose of assessing the influence of projected changes in acid deposition on water quality, are either acidified or judged potentially sensitive to acidification. The UKAWMN sites were also chosen to minimise the effects of local anthropogenic catchment based impacts.

Townsend *et al* (1983) reported on a study of thirty-four stream sites undertaken in 1976, relating a number of physicochemical variables to the structure of the benthic communities. A further study (Townsend *et al* 1987), examined community change in twenty-seven of the original thirty-four sites, and found indications of community persistence, particularly in the acid stream sites. There have been a number of other individual studies using one or more of the Ashdown Forest streams (Hildrew *et al* 1984; Hildrew & Townsend 1987; Groom & Hildrew 1989; Dobson & Hildrew 1992; Winterbourn *et al* 1985; Lancaster *et al* 1991), which cover many ecological aspects. Other extensive stream surveys in the UK include Wright *et al* (1984) and Ormerod & Edwards (1987).

With regards the UKAWMN stream sites, they were set up in 1988 following a report by the United Kingdom Acid Waters Review Group (UKAWRG) (Warren 1986). The aims of the report were five-fold: (i) to establish a comprehensive and representative picture of the distribution of acid waters in the UK, (ii) to review the causes of acidification and the mechanisms involved, (iii) to evaluate the extent of changes in the biota of acid waters, (iv) to estimate the extent to which these changes are due to acid depositions, and (v) to evaluate methods available for predicting the consequences of changes in deposition in the future. Fig 2.1 gives the location of the stream sites for the UKAWMN and Fig. 2.2 for the Ashdown Forest. Table 2.1 gives chemical data for both suites of sites. The setting up of the United Kingdom Acid Waters Monitoring Network in 1988 was a recommendation of the Acid Water Review Group with the objective of providing a long-term, high quality, chemical and biological database to facilitate the assessment of trends in surface water acidity in the UK.

In this chapter, I shall be looking at each suite of sites in turn, starting with the Ashdown Forest stream sites, one of which (Old Lodge 1) is included in the UKAWMN sites.

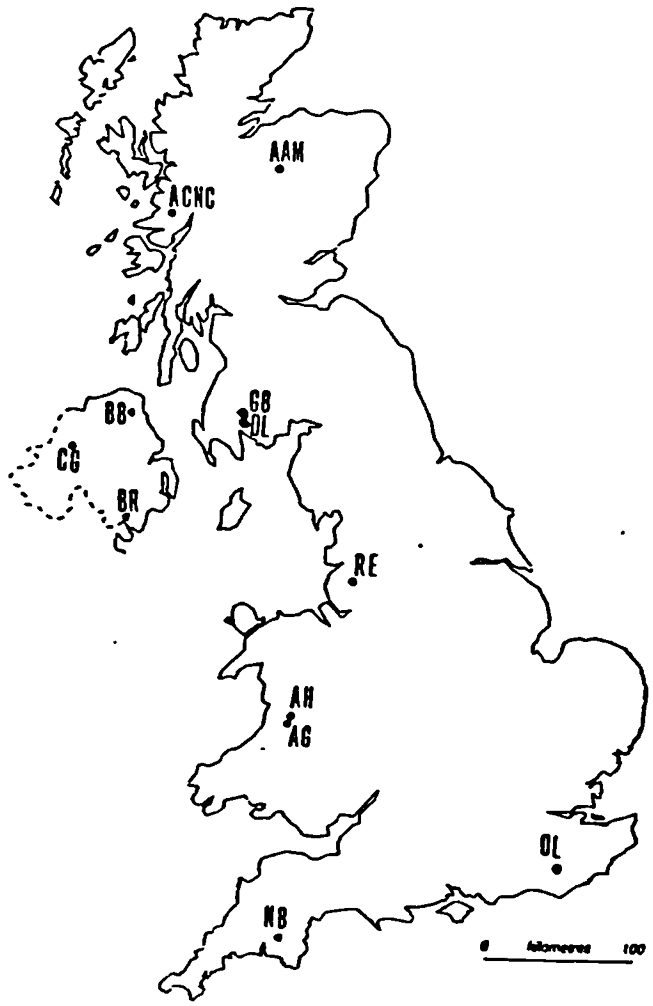


Fig 2.1: Location of the UKAWMN stream sites.

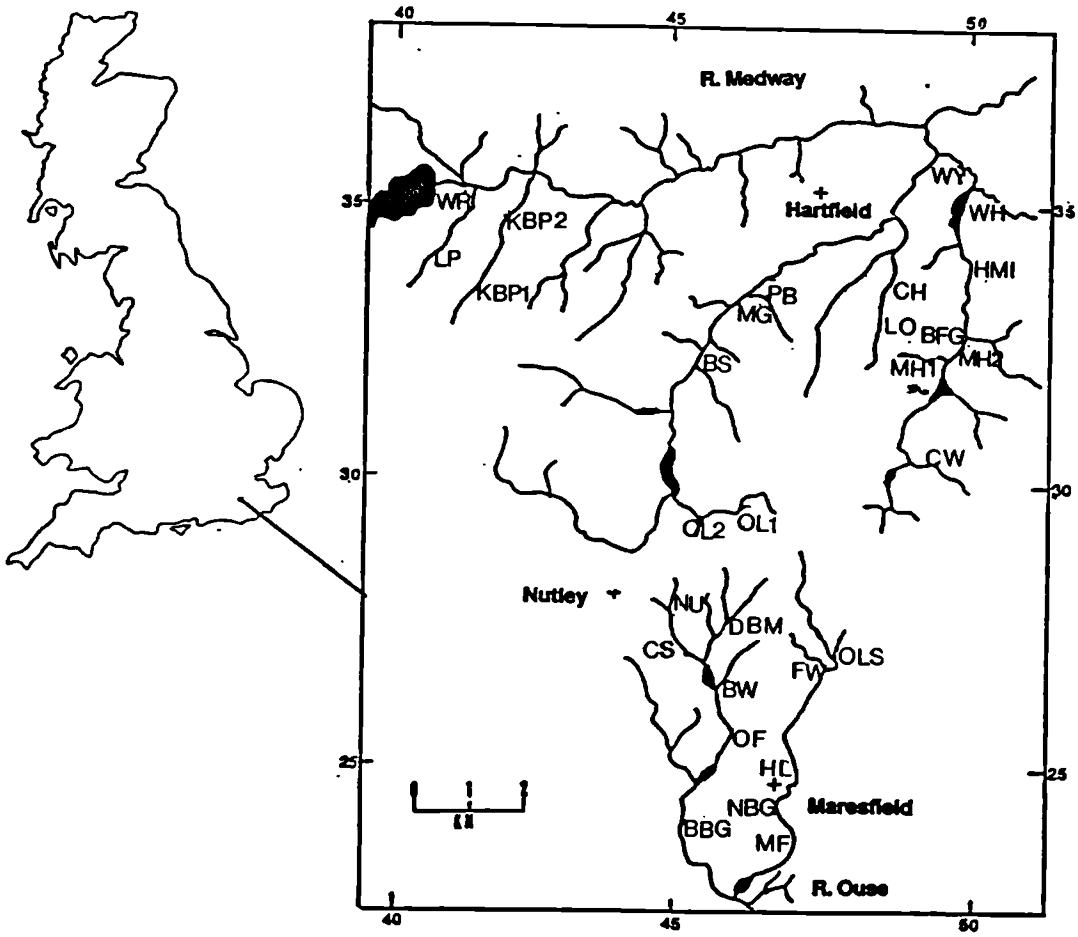


Fig 2.2: Location of Ashdown Forest stream sites.

A list of twelve sites for the UKAWMN are given below with site number in the monitoring network, its name, abbreviated name and grid reference. Overleaf a list of the Ashdown Forest sites are given, (site numbers here refer to numbers first ascribed by Townsend *et al* (1983).

Site No.	Name	Initials	Grid ref.
2	Alt a' Mharcaidh	AAM	NH 881045
3	Alt na Coire nan Con	ACNC	NM 793688
9	Dargall Lane	DL	NX 449786
23	Green Burn	GB	NX 481789
12	River Etherow	RE	SK 116996
*13	Ashdown Sands	AS	TQ 456294
14	Narrator Brook	NB	SX 568692
17	Afon Hafren	AH	SN 844876
•25	Llyn Brianne	LB	SN 824854
19	Beagh's Burn	BB	D 173297
20	Bencrom River	BR	J 304245
22	Coneyglen Burn	CG	H 640885

* This site is the same as 'Old Lodge' (Site 6 in the Ashdown Forest sites). See page 22.

• Llyn Brianne (LB) was replaced by Afon Gwy (AG) in 1991.

Site No.	Name	Initials	Grid ref.
1	Lavender Platt	LP	TQ 406339
2	Weirwood Road	WR	TQ 413347
3	Kidbrook Park 1	KBP1	TQ 417337
4	Kidbrook Park 2	KBP2	TQ 417330
5	Nutley Bridge	NBG	TQ 442287
*6	Old Lodge 1	OL1	TQ 456294
7	Old Lodge 2	OL2	TQ 456294
8	Chuck Hatch	CH	TQ 476334
9	Lone Oak	LO	TQ 475333
10	Crowborough Warren	CW	TQ 489304
11	Nutley	NU	TQ 449277
12	Cackle Street	CS	TQ 451272
13	Dodd's Bottom	DB	TQ 457273
14	Old Lands	OLS	TQ 476268
15	Fairwarp	FW	TQ 473264
18	Marden's Hill 1	MH1	TQ 496320
19	Marden's Hill 2	MH2	TQ 496321
20	Below friars Gate	BFG	TQ 498326
21	Old Forge	OF	TQ 458258
23	Batt's Bridge	BBG	TQ 453234
24	Hendall	HL	TQ 471259
25	Maresfield	MF	TQ 468241
26	Marsh Green	MG	TQ 461332
27	Pooh's Bridge	PB	TQ 471338
28	Half Moon Inn	HMI	TQ 499336
29	Withyham	WY	TQ 497358
33	Withyham Hall	WH	TQ 449353
34	Boringwheel Mill	BWM	TQ 457264
35	Broadstone Stream	BS	TQ 462259

* This site is the same as 'Ashdown Sands' (Site 13 in the UKAWMN). See page 21.

ENVIRONMENTAL DATA.

Table 2.1: Table giving the name, site number and mean pH, mean temperature (^{0}C) and mean conductivity (u S cm^{-1}) for 1990, for all the sites sampled. Llyn Brianne was replaced by Afon Gwy in 1991.

Ashdown Forest.

Site Name	pH	Temperature	Conductivity.
Lavender Platt	6.4	11.1	125
Weirwood Rd	6.7	12.7	202
Kidbrook Pk 1	5.9	12.0	153
Kidbrook Pk 2	5.5	11.5	222
Nutley Bridge	6.2	11.8	211
Old Lodge 1	4.5	11.8	95.5
Old Lodge 2	4.5	9.8	98
Chuck Hatch	5.0	11.6	112
Lone Oak	4.8	11.8	105
Crowborough Warren	6.7	12.3	216
Nutley	6.8	12.6	229
Cackle Street	6.6	11.8	230
Dodd's Bottom	6.4	12.7	130
Old Lands	6.8	13.1	158
Fairwarp	5.9	12.4	188
Marden's Hill 1	6.8	12.3	176
Marden's Hill 2	6.4	12.3	181
Below Friar's Gate	6.5	12.3	187
Old Forge	6.7	13.2	197
Batt's Bridge	7.0	13.4	225
Hendall	6.7	12.8	171
Maresfield	6.5	13.1	198
Marsh Green	6.6	13.2	134
Pooh's Bridge	6.6	13.1	168
Half Moon Inn	6.5	13.0	235
Withyham	6.8	13.3	227
Withyham Hall	6.9	13.2	273
Boringwheel Mill	6.8	13.7	199
Broadstone Stream	5.3	11.9	86

UKAWMN Sites.

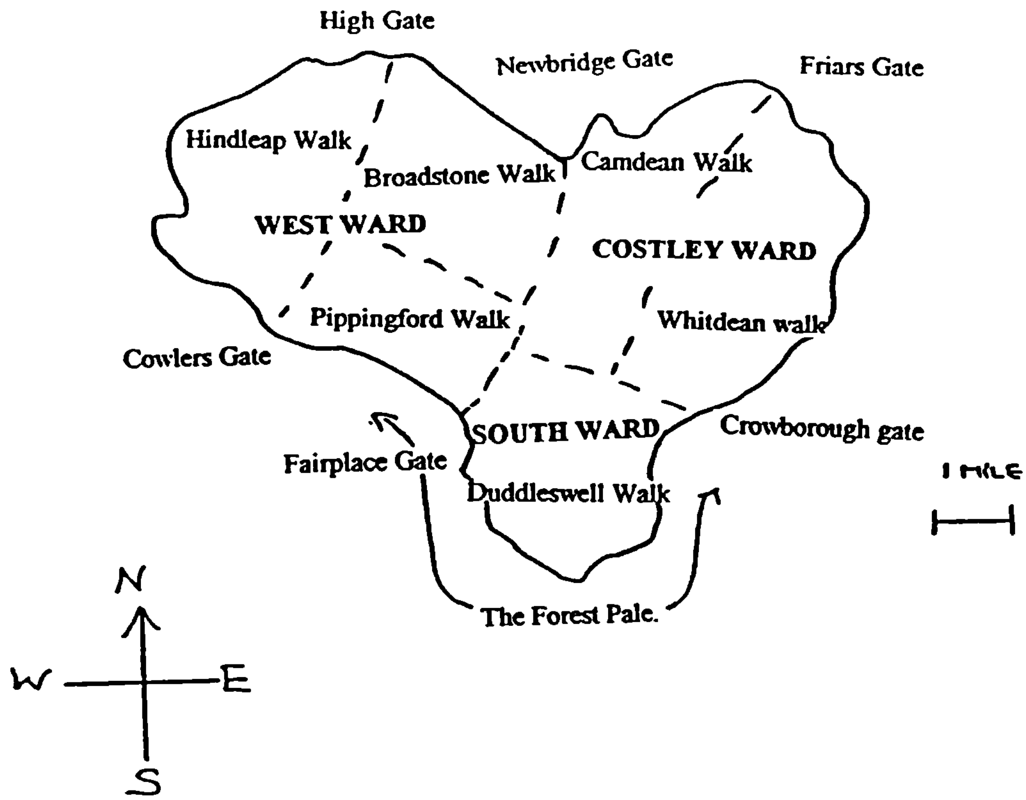
Site Name	pH	Temperature	Conductivity
Allt a' Mharcaidh	6.3	4.4	23.6
Allt na Coire nan Con	5.6	6.6	39.0
Dargall Lane	5.6	6.0	35.1
River Etherow	4.8	7.2	82.3
Ashdown Sands	4.5	9.8	95.5
Narrator Brook	5.7	9.2	47.8
Afon Hafren	5.4	6.4	38.6
Llyn Brianne	5.8	7.7	40.3 replaced by
Afon Gwy (1991)	4.9	7.8	41.3
Beagh's Burn	5.6	6.9	57.5
Bencrom River	5.2	9.8	44.3
Coneyglen Burn	6.3	6.4	56.6
Green Burn	5.5	6.1	36.2

ASHDOWN FOREST STREAM SITES.

2.ii. Historical Background.

The Medieval owners of Ashdown Forest, notably John of Gaunt, Duke of Lancaster, who held the forest from 1372-1399, saw the area primarily as a source of meat and a place in which to hunt the herds of red and fallow deer which thrived there. At some time before the end of the thirteenth century the forest was enclosed by a 'pale', which consisted of a bank surmounted by a wooden fence and with a parallel internal ditch. This was designed to allow the deer easy access to the forest but to make it difficult for them to jump out. Human access was via the many gates or 'hatches' some of which gave their names to settlements that survive today e.g. Colemans Hatch and Chuck Hatch. The forest was divided into three 'wards', each administered by foresters and each with a number of walks. The West Ward of the forest was made up of three walks, the Ward of Costly was made up of two and the South Ward had only one walk, that of Duddleswell. Figure 2.2 shows a map of the forest area up until 1693 (information from Ashdown Forest Centre, Forest Row). The keepers were housed in lodges and each walk had its own lodge, usually situated at the highest land available to provide extensive views. As the Master Forester was a person of standing, with other duties in the county, it was necessary to appoint a deputy to oversee the forest in his absence; the deputy was called the Rider and Ranger of Ashdown Forest - he 'ranged' on horseback over the whole forest, supervising the keepers of the wards and walks and the activities of the 'commoners', who held lands around the forest to which were attached certain rights to grazing and wood collection inside the pale.

The deer may have been an important feature of the forests but there were other valuable resources to be found. Since before the Romans, the area had been mined for iron and the forest was still of great importance for timber and iron-ore, which was needed in large quantities to supply the Wealden iron industry, during the sixteenth and seventeenth centuries. Constant vigilance by the commoners and keepers was needed to ensure that the forest trees and even the pale, did not disappear into the hands of the charcoal burners. The pits created by those digging for ore were often left open, endangering the forest's game and the commoner's cattle. In spite of complaints by the commoners, the iron industry in the Ashdown forest outlived the deer, only to collapse in the early eighteenth century due to competition from Scotland, Wales and the industrial north. It is still possible to find traces of the forest's 'Iron Age' - iron slag can still be found, sunken hollows remain and some streams are still coloured by the iron deposits. Places such as Boringwheel Mill (site 34), where the cannons were said to have been bored out, still exist, and another site related to the industry includes Old Forge Lane (site 21). There are other names that come from even further back (not including the names associated with the Wards and walks), such as Maresfield (site 25), from the Old English Meres field. This is an area that used to consist of pools or 'meres' downstream of a lake. Over the centuries, there was a decline in the care of the forest and a number of legal battles ensued over its ownership and use. An Act of Parliament, passed in 1885, placed the forest in the hands of Lord De La Warr (formerly Earls of Dorset), but some of the commoner's rights were upheld and the public were given legal right of access to specific areas of the forest for recreation. A Board of elected 'Conservators' administered the forest and they had the duty to preserve the forest's unique character for all time. Today the situation remains much the same, although few commoners graze their animals on the forest and the public now have the right, by Act of Parliament of 1974, to wander over the land administered by the Conservators. One of the main associations the public has for the Ashdown Forest is that of the childhood stories of Winnie the Pooh, by A.A. Milne. In fact, stream site 27 is Pooh's Bridge- where 'Pooh sticks' was played.



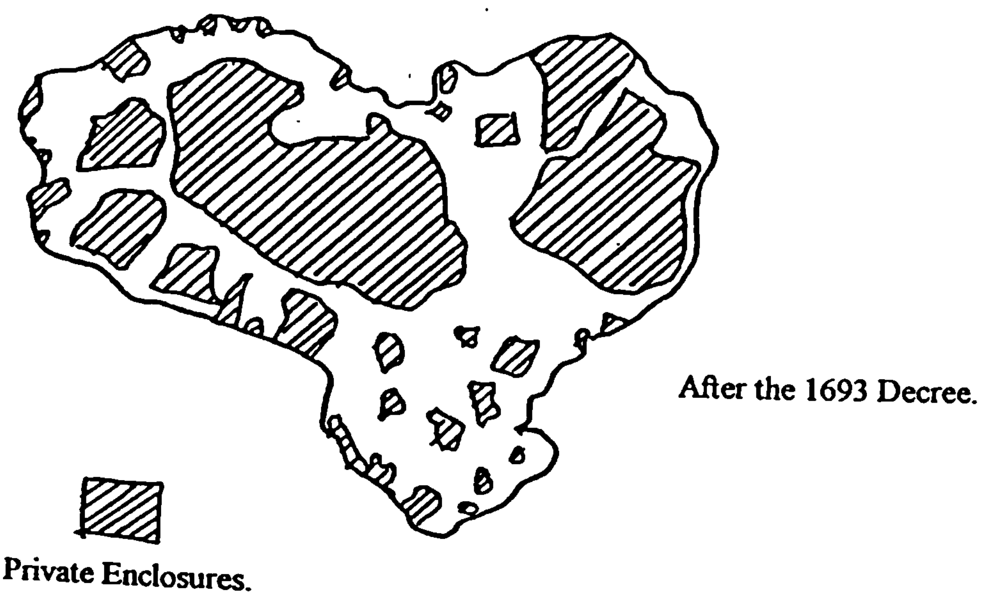


Fig 2.3: Map of the Forest.

The Forest's Wards and Walks.

Catchment details

The streams sampled in the Ashdown Forest are the headwaters of two rivers, the Medway, which flows north to join the Thames estuary, and the Sussex Ouse, which flows south to the English Channel at Newhaven. The watershed between the Medway and the Ouse bisects the study area. All the streams sampled lie in a group of hills in the centre of the Weald in south-east England and the geology is of soft fine sandstone (Ashdown sands) and Wadhurst clay, laid down in the Cretaceous period. Due to the historical land use of the area, much of the woodland is restricted to the steep sides of stream valleys and, in more recent years, there has been some conifer plantation. These wooded areas consist of mainly oak, *(Quercus robur)* with some hybrid oaks and hornbeam *(Carpinus betulus)* and beech *(Fagus sylvatica)*. The remaining common land, some 2590 ha, has not been improved and the vegetation is typically that of acid heath with *Calluna vulgaris* and *Erica tetralix*, with areas of gorse (*Ulex europaeus*) and the inevitable spread of bracken *(Pteridium aquilinum)*. In areas of wet heath *Sphagnum* spp occurs. There is some encroachment of open land by birch *(Betula pendula)* and Scots pine *(Pinus sylvestris)*. Annual rainfall in the area is on average c. 800 mm with wet deposited acidity of 0.10 kg H^+ ha^{-1} yr^{-1} and wet deposited non-marine sulphate of 4.99 kg S ha^{-1} yr^{-1}.

As described by Townsend *et al* (1983), the study area was confined to the more permanent streams of the Ashdown Forest found on the present common and enclosed areas on the Ashdown Sands. The original thirty-four stream sites were included in the survey after a drought, which eliminated any streams which dry up (seasonally). All samples in my study were taken from stony riffles, in the same area of the stream as was used in two previous surveys (Townsend *et al* 1983; Townsend *et al* 1987). I sampled twenty-nine of the original streams and these are listed by name and number in Table 2.1. The circumneutral streams generally tend to have wider, open channels and fewer channel obstructions, whilst the acid sites tend to be in wooded areas, with narrow untended channels. An example of a circumneutral site is Marsh Green (site number 26), and an example of an acid site is Broadstone Stream (site number 35), see photographs on page 32.

Details on physicochemical factors for each site are given in Table 2.1, based on water samples taken in the autumn and spring. Chemical surveys based on infrequent, spot samples have often been used to characterise stream sites in analyses of invertebrate communities (Townsend *et al* 1983; Townsend *et al* 1987; Ormerod & Edwards 1987). The assumption is that they give a sufficiently robust ordering of streams for this purpose. Stream chemistry, however, particularly at acid sensitive sites, is notoriously variable on short-term time scales (hours to days) (UKAWRG report, 1988). It is possible, therefore, for sites to be characterised wrongly on the basis of one or a few samples. On the other hand it is rarely practicable or affordable for large numbers of sites to be continuously or even very frequently monitored over long periods of time.

As a partial resolution of this dilemma, and to assess the likely importance of inadequate chemical sampling of the Ashdown Forest sites, I adopted a sampling strategy which can be referred to as a "seasonal window". For the four seasons of the year 1991 (spring, March; summer, June; autumn, September; winter, December) water samples were collected daily for seven days. Water temperatures were taken at the time of sampling and pH and conductivity measured, using the precautions and protocols adopted in the methodology of the UKAWMN (Juggins *et al* 1989). Five acid and five circumneutral sites were selected for this analysis. Table 2.2 gives the mean pH, conductivity and water temperature of seven days water samples for spring, summer, autumn and winter of 1991. In Fig 2.4 the results for pH sampled over seven days for the four seasons are given. They show the acid streams maintain a pH below 6.2 throughout the year - with a segregation of the two most acid sites (below 5.6), Old Lodge and Broadstone stream. Water temperature showed little variation between sites, although the acid streams were marginally lower. Four of the acid streams had conductivity readings below 140 uS cm^{-1}. Withyham, Lavender Platt and Nutley showed an increase over the year and Fairwarp had a decrease in conductivity. The conductivity data for the four seasons is given in Fig 2.5.

Table 2.2 Mean of seven days water samples for spring, summer, autumn and winter taken in 1991 at five acid and five circumneutral sites. There is little difference between the sample data taken over seven days compared with the annual spot samples given in Table 2.1 and the mean of the 'seasonal window' data given here.

pH

MONTH	SITE									
	WH	**MG**	**NU**	**BWM**	**MF**	**LP**	**CH**	**FW**	**BS**	**OL**
March	6.9	6.7	7.0	6.9	6.6	6.3	5.0	5.8	5.3	4.9
June	7.0	6.7	6.8	7.0	6.7	6.4	5.2	6.1	4.9	4.7
September	7.2	6.6	6.9	6.8	6.8	6.4	5.6	6.2	5.4	4.7
December	7.1	6.5	6.8	7.1	6.6	6.5	5.9	6.0	5.1	4.8

Conductivity

MONTH										
March	157	176	190	130	203	119	114	160	107	107
June	169	190	188	177	189	132	133	156	95	114
September	184	196	212	195	206	136	133	145	102	99
December	204	123	215	219	123	132	120	115	113	107

Temperature

MONTH										
March	9.5	9.5	9.5	10.0	9.5	10.0	9.5	9.5	9.2	9.5
June	11.5	10.5	10.5	10.3	10.4	11.0	10.5	10.5	10.2	10.3
September	10.0	10.0	10.0	9.5	10.0	10.0	10.0	9.5	9.4	9.5
December	2.0	1.5	2.1	2.0	2.0	2.0	2.0	1.9	1.3	1.4

The data presented in Table 2.2 are for ten sites only. When compared with the spot samples given in Table 2.1 for the same sites, there is broad agreement. Although there is some variability, particularly over the four seasons, the range is within acceptable limits, particularly for the acid sites. This gives one confidence that the sites are ordered correctly from the occasional spot samples.

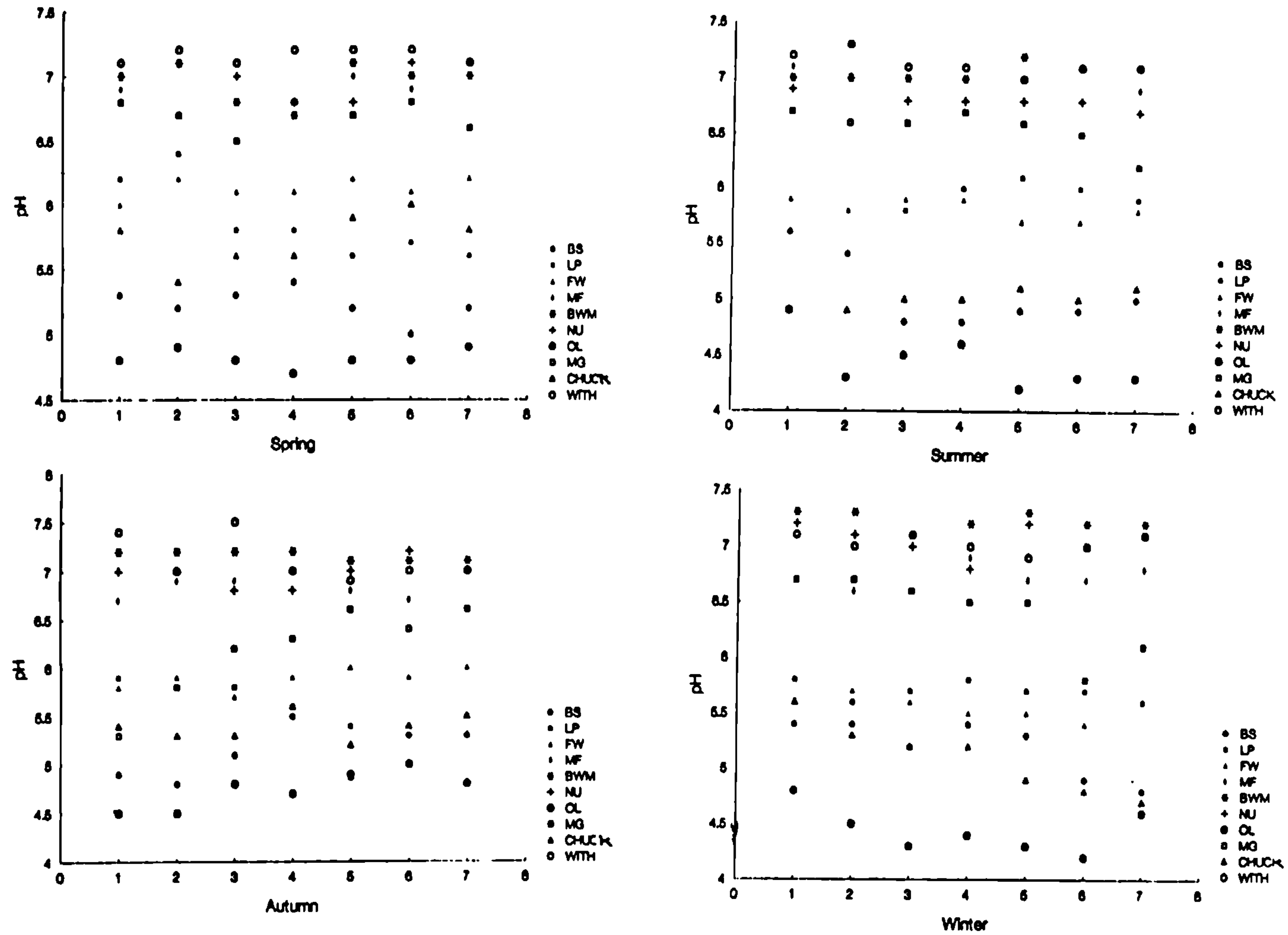


Fig. 2.4: Daily recordings of pH for seven days, four times a year, taken in (1991). Ten stream sites were chosen, five acid and five circumneutral. The acid sites include Broadstone stream, Old Lodge, Fairwarp, Chuck Hatch and Lavender Platt (BS, OL, FW, CHUCK & LP). The circumneutral sites include Maresfield, Marsh Green, Nutley, Withyham and Boringwheel Mill (MF, MG, NU, WITH & BWM).

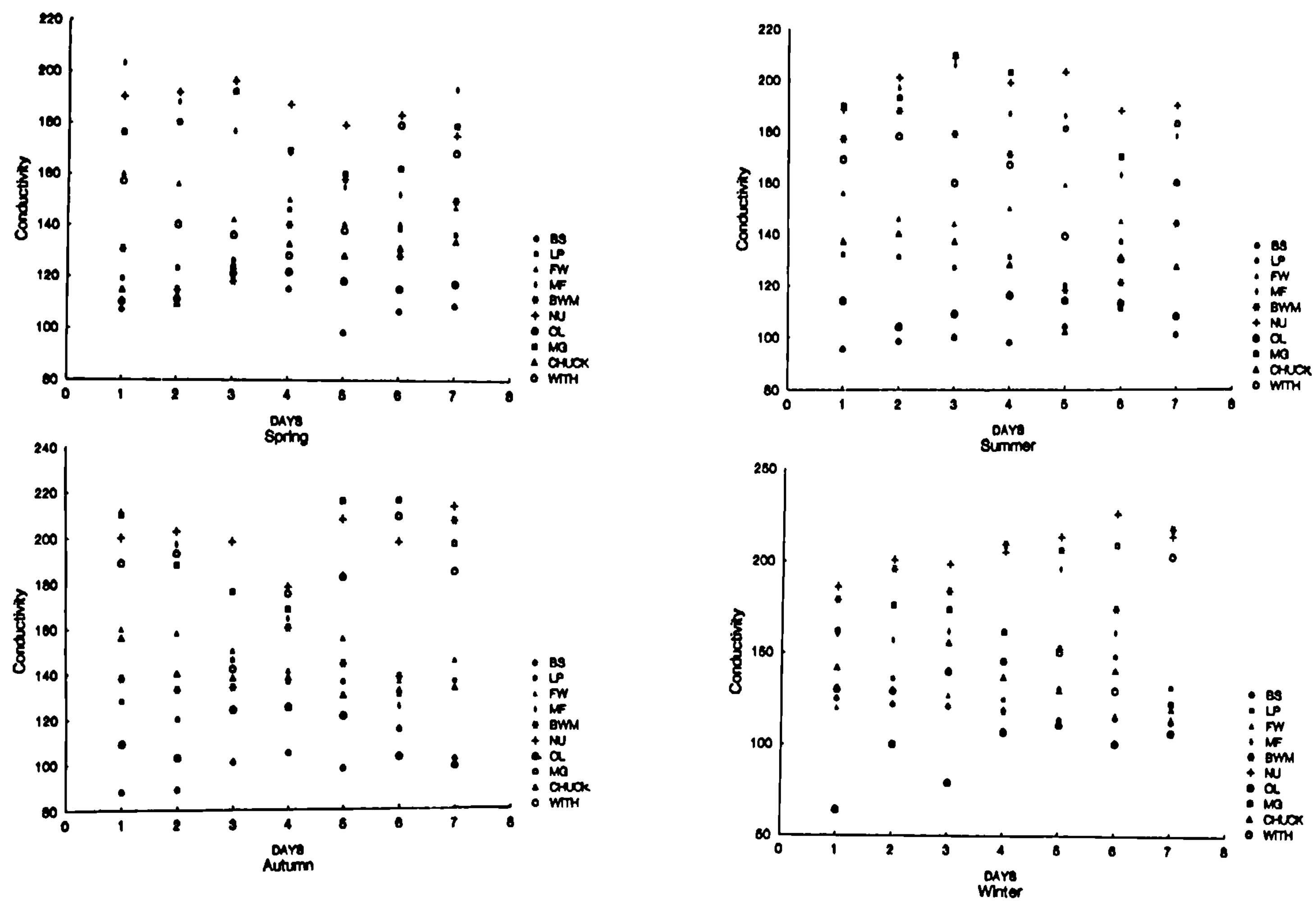


Fig. 2.5: Daily recordings of Conductivity ($\mu S\ cm^{-1}$) taken on seven consecutive days during the four seasons of 1991. The acid sites are: Broadstone stream, Old Lodge, Fairwarp, Chuck Hatch and Lavender Platt (BS, OL, FW, CHUCK & LP), and the circumneutral sites are: Maresfield, Marsh Green, Nutley, Withyham and Boringwheel Mill (MF, MG, NU, WITH & BWM).

Marsh Green, a circumneutral stream.

Broadstone stream, an acid stream.

2.iii. UKAWMN STREAM SITES.

The Scottish stream sites in the network consist of two streams in the Galloway area of south-west Scotland and one each in the north-west and the north-east. There are three further streams in the network in Northern Ireland, two in Wales, and one each from the south-east, the south-west and north-west of England. This makes a total of twelve stream sites (Fig 2.1), of which one (Ashdown Sands, also known as Old Lodge1) is common with the Ashdown Forest suite of sites. Each network site will be described separately.

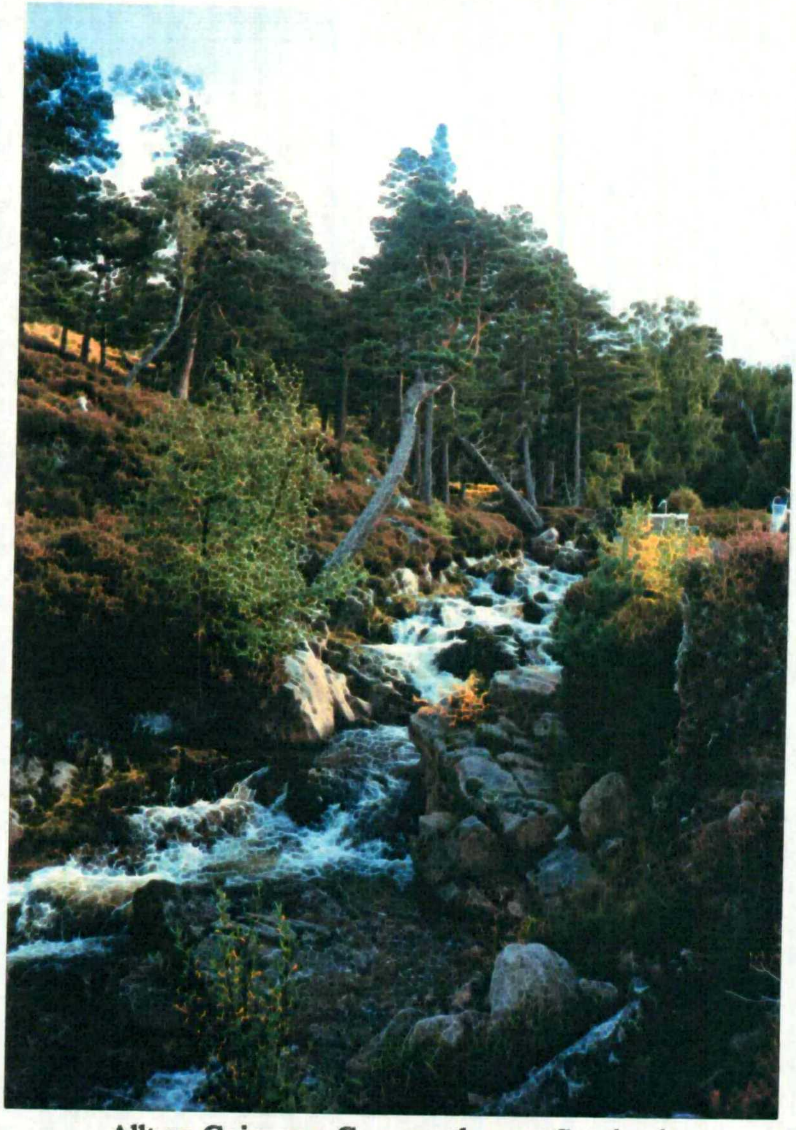
SCOTLAND

ALLT A' MHARCAIDH.

The catchment lies on the western side of the Cairngorm Mountains, has an area of 998 ha and drains to the river Feshie, a tributary of the River Spey. The sampling station is at 325 m in a catchment that rises to 1111 m at Sgoran Dubh Mor. Alpine and peaty podsols cover 60% of the area and the remainder is blanket peat. The underlying geology is intrusive biotite-granite of lower Old Red Sandstone. Vegetation in the catchment is characterised by a heather/fescue grass mix with a few native pine woods (10%) interspersed along the lower reaches. This area is part of the Cairngorm National Nature Reserve and land-use is confined to deer grazing. The annual rainfall in 1988 was c. 1200 mm in an area which receives a wet deposited acidity of 0.25 kg H^+ ha^{-1} yr^{-1} and wet deposited non-marine sulphate of 3.83 kg S ha^{-1} yr^{-1}. The gradient is steep throughout the upper catchment. Exposed bedrock, rapids, waterfalls and large boulders characterise the channel section used for monitoring. During periods of low flow the stream bifurcates leaving large parts of the 10 m wide channel exposed. Flow, pH and conductivity are monitored continuously at 20 minute intervals and the pH range is 6.1-6.3.

There are epilithic diatoms present, dominated by the circumneutral taxa *Achnanthes minutissima* and *Synedra miniscula,* and the macrophytes are almost

Allt a' Mharcaidh, in the Cairngorms, Scotland.



Allt na Coire nan Con, north-west Scotland.

exclusively bryophytes. The macroinvertebrate fauna is abundant and diverse. The mayflies *Rhithrogena semicolorata* and *Baetis* spp. are found, taxa which are intolerant of very acid waters. The stonefly fauna consist of the detritivores *Brachyptera risi, Protonemura meyeri, Amphinemura sulcicollis* and the predator *Isoperla grammatica*. Trout, up to three years old, and salmon, up to two years, have been recorded.

ALLT NA COIRE NAN CON.

The catchment for this stream site lies in the Strontian region of western Scotland and drains into the River Polloch, an inflow to Loch Shiel. The catchment covers 790 ha and rises from 10 m at the sampling point to a peak of 756 m. The dominant soil types are peats, peaty podsols and peaty gleys. In the upper reaches of the catchment there is some peat erosion. The underlying geology is mainly schists and gneisses of the Moine series. Approximately 50% of the catchment is covered by conifers, mature spruce and larch. The lower slopes have been felled to allow a road through, and the remaining area, the upper slopes, are dominated by *Molinia,* with *Calluna* and *Sphagnum* in wetter areas. The altitude range is from 10 m to 700 m at the headstream. The channel is 5-6 m wide at the sampling point and consists of exposed bedrock, boulders, waterfalls and rapids. The sides of the stream are shaded by alder and rowan trees. Flow, pH and conductivity are monitored at 30 minute intervals. Streamwater has a pH range of 5.8-5.9. Epilithic diatoms consist of mainly one species, *Achnanthes saxonica,* which is indicative of mildly acid waters associated with afforested catchments. The macroinvertebrate fauna includes the Ephemeroptera, *Rhithrogena semicolorata* and *Baetis spp.* Simuliidae are very abundant and the Plecoptera fauna includes *Perlodes microcephala*. Both young trout and salmon have been recorded. Total annual rainfall is 2600 mm in an area with a wet deposited acidity of 0.76 kg H^+ ha^{-1} yr^{-1} and wet deposited non-marine sulphate of 16.11 kg S ha^{-1} yr^{-1} .

DARGALL LANE & GREEN BURN.

These sites are within a short distance of each other, and are treated as the same with regards to catchment and stream characteristics. The catchment is a sub-catchment of Loch Dee, Galloway south-west Scotland. The sampling station is at 260 m and the catchment rises to 761 m at Lamachan Hill. The underlying geology is complicated and includes Silurian and Ordovician greywacks, shales and mudstone, and granite/gneiss intrusions. The dominant soil type is podsolic, covering approximately 80% of the area, with peaty gleys and blanket peat.

The altitude range is from 260 m at the sampling station to 630 m at the headwaters. At the sampling station the channel is 4 m wide and with a boulder and cobble substratum. Flow, pH and conductivity are monitored at hourly intervals. The streams are acid, with an annual pH range of 5.3-5.6. There are four epilithic diatom species found which are indicative of mildly acid conditions, *Eunotia naegelii, Eunotia incisa, Peronia fibula* and *Tabellaria flocculosa*. Approximately 25% of the stream bed has macrophytic cover and the species-poor vegetation is dominated by the leafy liverwort *Scapania undulata,* although *Nardia compressa* also occurs. Filamentous green algae are also locally abundant.

The macroinvertebrates are diverse and abundant and consist of detritivorous Plecoptera such as *Leuctra inermis.* There are no records of Ephemeroptera, though a reasonable population of trout, up to four years old, inhabit this stretch of water. Total annual rainfall is around 2500 mm and the wet deposited acidity was 0.46 kg H^+ ha^{-1} yr^{-1} and wet deposited non-marine sulphate was 14.36 kg S ha^{-1} yr^{-1} .

Dargall Lane, in Galloway, Scotland.

Green Burn, in Galloway, Scotland.

ENGLAND

RIVER ETHEROW

This site drains an area of 1300 ha and flows into the Woodhead Reservoir. The highest point of the catchment is Bleaklow head at 633 m. The underlying geology is Millstone Grit and the majority of the soils are peaty podsols. The vegetation is moorland, with both rough and improved grassland. Vegetation is dominated by *Calluna, Vaccinium, Agrostis* and *Molinia*. There are a few trees, mainly silver birch and sessile oak. The lower catchment is used for sheep grazing, while the upper area is grouse moor, where heather is managed by burning on a rotation scheme. The main A 628 trunk road passes through the catchment and close to the sampling station, which may have an effect on stream chemistry.

The altitude range is from 280 m at the sampling station to 620 m at the headwaters. The width of the channel which is sampled is 10 m and consists of a substratum of shallow bedrock ledges, large boulders and cobbles. The flow, pH and conductivity are recorded at fifteen minute intervals and the stream has a mean annual pH of 4.8. Diatom species include *Eunotia exigua, E. incisa* and *E. rhomoidea,* while the liverwort *Scapania undulata* occurs on exposed bedrock. Macroinvertebrates include the Plecoptera *Leuctra inermis* and one species of Ephemeroptera, *Ameletus inopinatus.* The river is fishless and, with the fishless reservoir immediately below, it is unlikely that recolonisation will occur. The total annual rainfall in 1988 was 1600 mm and the wet deposited acidity was 0.64 kg H^+ ha^{-1} yr^{-1} and wet deposited non-marine sulphate was 16.80 kg S ha^{-1} yr^{-1} .

OLD LODGE.

This site also comes into the Ashdown Forest suite of sites and so will only be briefly mentioned here. The underlying geology is Ashdown Sands and the soils are typically podsolic. The catchment area is deciduous woodland and heathland vegetation. There has been no land-use disturbance for at least the last 200 years. The channel is narrow with fallen tree limbs and has a bed of boulders, cobbles and gravel. There is only one diatom recorded, the acidobiontic *Eunotia exigua.* Macroinvertebrates are few and characteristic of acid streams.

NARRATOR BROOK.

This stream site lies in the Dartmoor National Park. The catchment covers 475 ha and drains into the Burrator Reservoir. The altitude at the reservoir inflow is 225 m and the maximum altitude is reached at Cairn Eylesbarrow at 456 m. The underlying geology is granite and the soils are entirely podsolic. The vegetation consists of two thirds *Molinia* dominated blanket bog with acid grassland. Conifers and deciduous woodland and valley bog make up the rest. Sheep, cattle and ponies graze the area. The stream section sampled is located on an open floodplain and the substratum is cobbled upstream and there are narrow reaches which are fast flowing with deep pools where sand and gravel accumulates. Water chemistry is sampled monthly and the mean pH is 5.6. The epilithic diatoms are diverse and include circumneutral species such as *Achnanthes minutissima,* together with some acid tolerant species of *Eunotia.* There are numerous bryophytes with the moss *Rhynocostegium riparoides* particularly abundant. Macroinvertebrates are abundant and include species intolerant of acid conditions. Trout densities are the highest of all the UKAWMN stream sites - 0.520 +/- 0.072 m^2. In 1988 the area received c.1800 mm of rainfall and the wet deposited acidity was 0.25 kg H^+ ha^{-1} yr^{-1} with a wet deposited non-marine sulphate of 6.35 kg S ha^{-1} yr^{-1} .

<u>WALES</u>

AFON HAFREN.

This site lies in the Cambrian Mountains of mid-Wales and from its confluence with the Afon Hore it forms the headwaters of the River Severn. The catchment area is 358 ha and rises from 355 m at the sampling station to 690 m at Blaenhafren. The soils are mainly podsols and organic peaty soils. The underlying geology consists of Ordovician grits and Silurian mudstones and shales. Up to 50% of the area is planted

Narrator Brook, in Dartmoor National Park.

Afon Hafren, in the Cambrian Mountains of mid-Wales.

with conifers, mainly Sitka and Norway spruce. The channel width at the sampling station is c. 3.5 m and the substratum consists of boulders, cobbles and pebbles. Stream chemistry is sampled monthly and the pH is sampled continuously with a mean pH range of 5.0-5.4. There are no Ephemeroptera recorded and no fish have been caught, although local sources suggest that fish were present in the stream in the 1940s. Total annual rainfall is in the region of 2500 mm, with wet deposited acidity of 0.27 kg H^+ ha^{-1} yr^{-1} with a wet deposited non-marine sulphate of 7.54 kg S ha^{-1} yr^{-1} .

NANT Y GRONWEN or LLYN BRIANNE.

This site lies in the Cambrian Mountains of mid-Wales and drains via the Camddwr into the Llyn Brianne Reservoir. The catchment is 77 ha and rises from 330 m at the sampling station to 450 m. The underlying geology is dominated by Lower Silurian mudstones interbedded with well sorted silts and fine, quartz-dominated sandstones. The soils of the area are peats, but podsols, gleys and rankers are also present.The vegetation is moorland and used for rough sheep grazing. The altitude ranges from 330 m to 386 m at the headwaters. The stream channel is narrow (1-2 m) with a shallow reach and many small rapids. Water chemistry is analysed monthly and pH is monitored continuously. The pH range is 5.7-5.9. The macroinvertebrate fauna is poor and Ephemeroptera are absent. Annual rainfall is in the region of 1780 mm and wet deposited acidity is 0.27 kg H^+ ha^{-1} yr^{-1} with a wet deposited non-marine sulphate of 7.42 kg S ha^{-1} yr^{-1} . This stream was withdrawn from the Monitoring Network in January 1991 at the request of the landowner and was replaced by the Afon Gwy.

AFON GWY.

This site lies to the east of Plynlimon in central Wales and forms part of the headwater system of the River Wye. The catchment area is 210 ha and rises from 440 m at the sampling station to 730 m. Soils are mainly peats and peaty podsols and the underlying geology is one of Lower Palaeozoic mudstones, shales and grits of the Gwestyn and Van formations, overlain in places by locally derived glacial drift. The vegetation is moorland supporting rough sheep grazing in the summer. Water chemistry is analysed monthly and pH measured continuously, having a mean value of 4.9. The area received a rainfall of c. 2500 mm, with a wet deposited acidity of 0.27 kg H^+ ha^{-1} yr^{-1} and a wet deposited non-marine sulphate of 7.54 kg S ha^{-1} yr^{-1} .

NORTHERN IRELAND

BEAGH'S BURN.

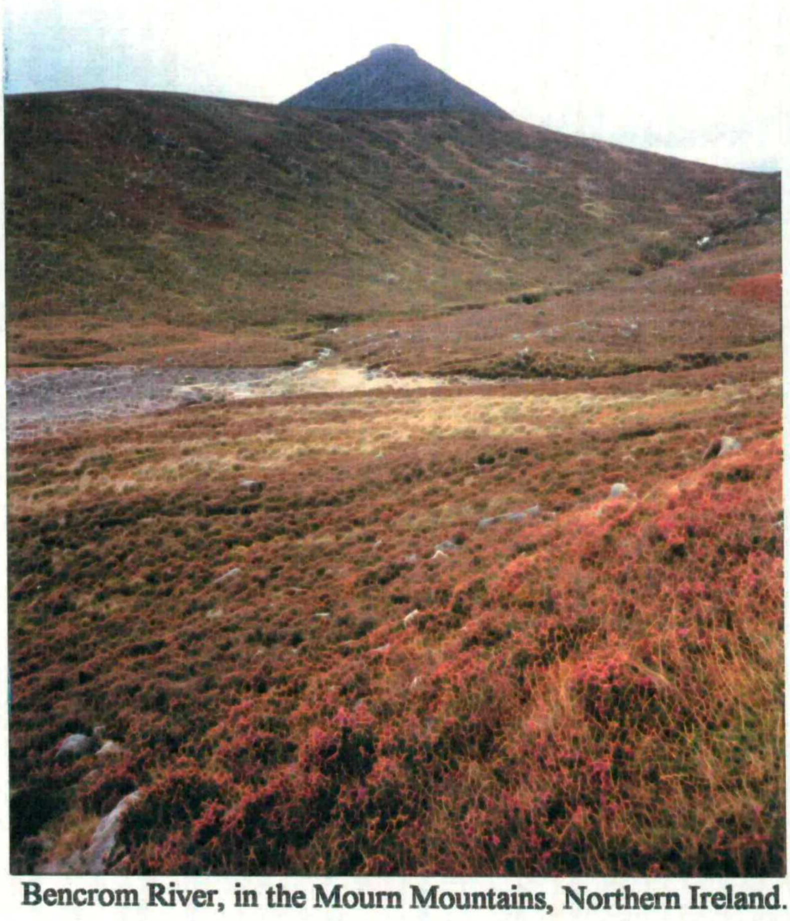
Situated in the Glens of Antrim in north eastern Northern Ireland, the catchment area is 273 ha and rises steeply from 150 m, above the confluence with the Glendun River, to 397 m at Oghtbristacree. The major soil type is one of blanket peats and the underlying geology consists of quartz-schists of the Glendun series.

Deciduous trees grow on the banks of the stream, otherwise the vegetation is of moorland species. The channel is narrow, approximately 2-4 m wide with a substratum of bedrock, boulders and cobbles. There is no continuous monitoring at any of the Northern Ireland sites, but chemical analysis is carried out monthly. The mean streamwater pH is 5.6. The invertebrate population is sparse and species poor, and there are no Ephemeroptera recorded. Annual rainfall is c.2500 mm, with wet deposited acidity of 0.25 kg H^+ ha^{-1} yr^{-1} and a wet deposited non-marine sulphate of 12.51 kg S ha^{-1} yr^{-1} .

BENCROM RIVER.

This stream site lies in the Mourne Mountains of county Down. The catchment area is 298 ha rising from 140 m, where the river meets the Silent Valley Reservoir, to 700 m at Slieve Meelbeg. The soils are mainly blanket peats and the underlying geology is one of fine grained granite with localised boulder clay drift. The moorland vegetation of the area is utilised for sheep grazing. The sampling station is immediately upstream of the confluence with the Silent Valley Reservoir and comprises a boulder strewn channel with many rapids. Mean annual pH is 5.1, and the river has a species poor macroinvertebrate community. Trout of all age classes have been caught here.

Coneyglen Burn, in the Sperrin Mountains, Northern Ireland.



Bencrom River, in the Mourn Mountains, Northern Ireland.

Annual rainfall is c. 1700 mm, with a wet deposited acidity of 0.25 kg H^{+} ha^{-1} yr^{-1} and a wet deposited non-marine sulphate of 12.51 kg S ha^{-1} yr^{-1}

CONEYGLEN BURN.

The Coneyglen Burn lies in the Sperrin Mountains of central Northern Ireland. The catchment area is 1414 ha, rising from 230 m at the sampling station to 562 at Carnanelly. The soil type is mainly blanket bog and the underlying geology is one of schists of the Mullaghcarn series. The vegetation of the catchment is one of planted conifers (5%) and grazed moorland. Mean pH is 6.3. The channel at the sampling station is straight, 4 m wide and has a substratum of bedrock and boulders. Macroinvertebrates are species poor, characterised by the plecopteran *Siphonoperla torrentium*. Trout of the year classes of 0+ to 2+ have been recorded. Annual rainfall is c. 1700mm, with a wet deposited acidity of 0.25 kg H^{+} ha^{-1} yr^{-1} and a wet deposited non-marine sulphate of 12.51 kg S ha^{-1} yr^{-1}

UKAWMN Flow data.

The flow regime plays a major role in structuring habitat conditions for stream insects and obviously the more frequent the measurements in the record, the more ecologially pertinent the information that is available. Resh *et al* (1988) looked at the role of disturbance in stream ecology, and in particular the effects of flow, by using long term hydrological data to quantify the predictability of the events. They looked at the geographical patterns of disturbance and noted that, although unusually high discharge was considered a natural phenomenon common to all areas, the impact of spates varies among sites. For instance, in high gradient streams spates may be catastrophic, resulting in bank erosion, scouring of the substratum and loss of biota and habitat. At the other end of the scale, drought will directly impact on all factors dependent on discharge, such as dissolved and organic matter, and plant and animal communities. Flow data was obtained from various bodies within the UK who are continuously monitoring the discharge of certain stream sites within the UKAWMN. Mean monthly flow data is given for seven sites from 1987 to 1992. The records are not complete for all stream sites.

Channel stability was also recorded using the Stream Reach Inventory and Channel Stability Rating, the Pfankuch score. This is a hardy, if rather gross, estimate of channel stability derived by the US Forestry Department, where a stream site is assessed and a score allocated for a number of features, the overall score being the Pfankuch rating.

Channel stability rating.

The Pfankuch score is obtained by assessing certain physical features of the stream channel. These include for the upper bank, the bank slope gradient, percentage of vegetation cover and for the lower banks, capacity, erosion, bar formation and obstructions to flow. For the stream bottom, particle size, an estimate of particle packing, algal cover, and how rough or smooth the stones are. Each of the divisions are given a score and the columns are added up. The total scores give a Pfankuch rating.

Pfankuch scores.

The scores were recorded from 1989 to 1991 for the UKAWMN stream sites and are given in Table 2.3.

The scores range from 1-38, Excellent, 39-76, Good, 77-114, Fair and 115+ Poor.

Table 2.3: Pfankuch scores: Channel stability rating for three consecutive years, 1989-91. Allt a' Mharcaidh, Allt Coire nan Con and Bencrom River were the only stream sites to have a consistent rating of Good. None of the sites were classed as excellent.

Site	Year 1989	1990	1991	Rating.
Old Lodge	67	75	77	G G F
Allt a' Mharcaidh	63	72	45	G G G
Narrator Brook	50	65	80	G G F
Llyn Brianne	81	100	-	F F
Afon Gwy	-	-	84	F
Bencrom River	69	69	63	G G G
Coney Glen	67	68	82	G G F
Beagh's Burn	46	76	110	G G F
Green Burn	78	87	68	F F G
Dargall Lane	74	94	71	G F G
R. Etherow	81	97	72	F F G
Allt Coire nan Con	60	68	53	G G G

Flow data.

Flow data were obtained from the Institute of Hydrology, at Wallingford and the Department of Agriculture & Fisheries Scotland (DAFS), Pitlochry. Only seven streams have flow determined continuously, and the frequency with which data is coded varies.

Site	Frequency interval	Method
Allt a' Mharcaidh	20 minutes	pressure transducer to a data logger.
Allt Coire nan Con	30 minutes	float recorder - stage, stored on data logger.
Dargall Lane	Hourly	Float recorder
Green Burn	Hourly	Float recorder.
R. Etherow	15 minutes	Float, to measure stage.
Narrator Bk	Monthly abstracted from continuous.	Flume; float to measure stage.
Afon Hafren	15 minutes	Flume, stage/discharge.
LLyn Brianne	15 minutes	Stage, on pressure transducer, data logged.

Data was accessed from computer disk and spreadsheets. Mean monthly flow was calculated for the total run of data. This varied for each site, for example, we have six years data for Green Burn but only three plus years for the River Etherow. Mean monthly flow was plotted over time, giving an indication of temporal variability.

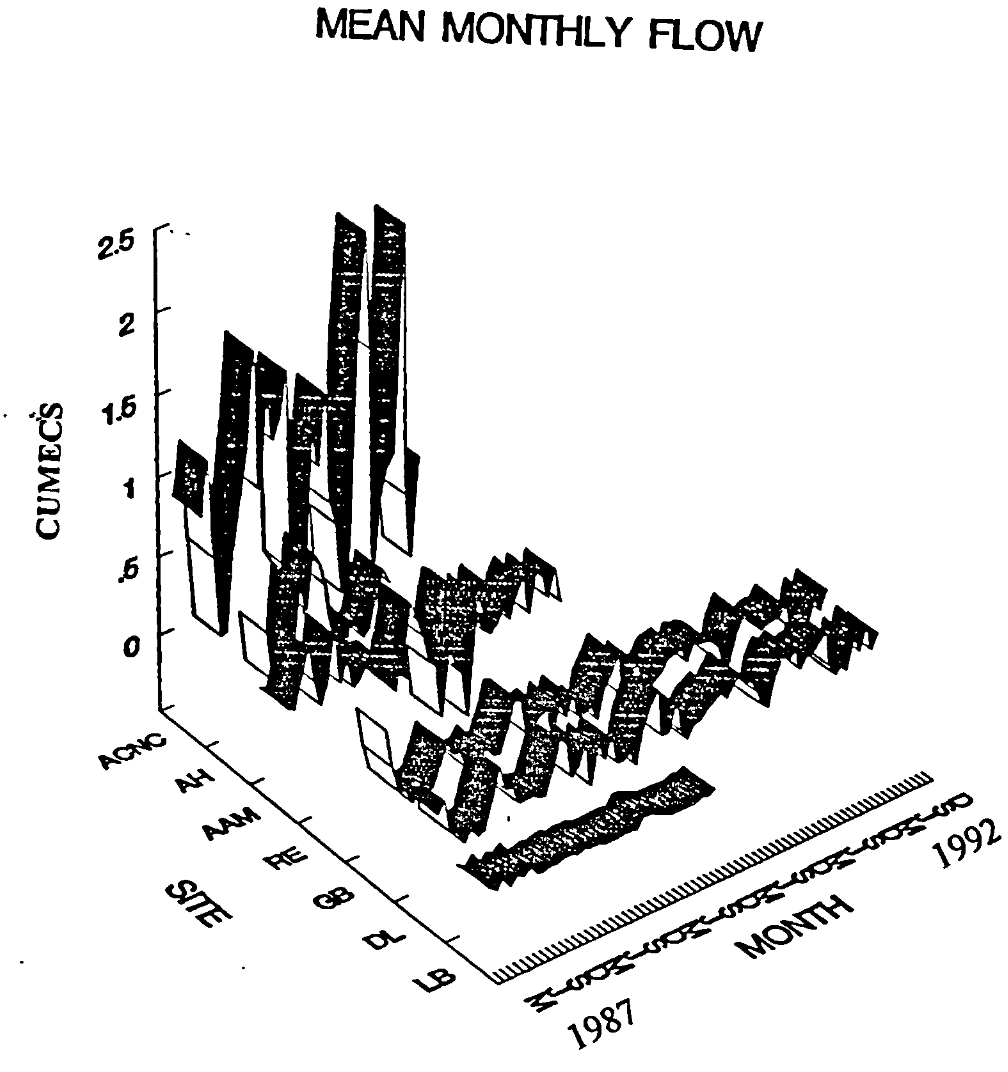


Fig 2.6: **Mean monthly flow in cumecs (cubic metres per second), for seven UKAWMN sites, from 1987-1992. Some sites only have two years data. Llyn Brianne has consistently low flow while others, like Alt Coire nan Con, are highly variable. Sites are listed by initials, LB (Llyn Brianne), DL (Dargall Lane), GB (Green Burn), RE (River Etherow), AAM (Alt a' Mharcaidh) and ACNA (Alt Coire nan Con).**

Types of river regimes can be identified by the shape of their annual hydrograph and according to the season of peak flow. In Fig 2.6, mean monthly flow data is given for seven sites from 1987 to 1992. The records are not complete for all stream sites. Llyn Brianne has a consistently low flow regime, whereas others, like Allt Coire nan Con, are highly variable. Abiotic factors may play a more important role in structuring stream benthic communities in streams with highly variable and/or unpredictable flow regimes. Discharge has an effect on substratum, food supply and dissolved oxygen levels, and therefore determines habitat conditions.

The channel stability rating or Pfankuch score has rather limited application. None of the stream sites had an excellent score, Good to Fair being the common ratings. From observation on different sampling occasions, the channels were certainly very variable and, when in flood, bank collapses were witnessed.

CHAPTER 3.

COMPARISON OF TWO SAMPLING METHODS.

3.i. INTRODUCTION.

Base line data on benthic invertebrates from 34 Ashdown Forest stream sites were first compiled in 1976 by Townsend *et al* (1983). In 1984 this was added to by Townsend *et al* (1987), and in 1989 my data was combined with the two previous surveys to give data collected on three occasions over a period of fourteen years. Having the information on the benthic invertebrates populations from these stream sites enables us to evaluate whether or not changes have occurred from one sampling occasion to the next. In addition to this, the Acid Waters Monitoring Network was specifically set up to detect change over time. This is done by having a programme, planned ahead of time, using the appropriate variables - in other words a monitoring programme. We use monitoring as an essential element of environmental impact assessment as it serves as a basis for determining the extent of changes which are development-induced, and for testing the effect of predicted impacts. In addition, data from monitoring programmes can provide a vital source of case history information that can be used in later, similar assessments (Rosenberg *et al* 1981). Biological and ecological monitoring also has an important role to play in the management of animal and plant communities for conservation purposes. Without monitoring changes in natural communities, species status and the effects of habitat loss, we have nothing on which to base good conservation practices.

Since the 1970s, there have been some major initiatives in monitoring and surveillance programmes, such as GEMS (Global Environment Monitoring Systems), run by UNEP (United Nations Environmental Program) based in Nairobi. These have tended to be in the area of assessing environmental quality, dealing with pollution, energy and other resources, rather than biological and ecological monitoring. By 1982, monitoring programmes supported by UNEP included work dealing with climate, the long range transport of pollutants, ocean monitoring and renewable terrestrial resources (Holdgate *et al* 1982). A British Ecological Society (B.E.S) workshop held for young ecologists supported the case for long term ecological monitoring as a main research priority (Hassell 1989). However, lack of financial resources has prevented all but a few projects getting off the ground, an example being the 1984 Ecological Data Unit within the Institute of Terrestrial Ecology (ITE).

There have also been initiatives by individual organizations such as the British Trust for Ornithology, whose common bird census for farm and woodland species was established in 1961. Other studies have been carried out retrospectively and these include using the egg shell index (based on the weight of the egg divided by the length times the width of the egg) to assess the change in shell thickness from 1947 onwards. The reduction in egg shell thickness has been linked with the use of DDT (Ratcliffe 1980). For aquatic systems the use of palaeolimnological indicators, such as diatom species, have been used to show changes in water acidification since the industrial revolution (Batterbee *et al* 1990). Information from these monitoring programmes becomes more and more valuable with time, not only in terms of understanding natural processes, but also in terms of providing a baseline for comparisons when disturbance or perturbations occur. Strayer *et al* (1986) lists four classes of ecological phenomena appropriate for long-term ecological studies.

1: Slow processes, such as forest succession and some vertebrate population cycles.

2: Rare events, perturbations such as fires, outbreaks of pests or disease.

3: Subtle processes, where year to year variance is larger than the long term trends, such as those found in the biogeochemistry of an aggrading forest (Likens 1983).

4: Complex phenomena and intricate ecological relationships in biotic communities.

Although not all long-term biological and ecological studies could be said to be examples of monitoring, there are characteristics which are common to both monitoring and long-term studies. Obviously the decision about the most appropriate time scale for a monitoring programmes should be linked with the objectives of the monitoring activity. The importance of linking objectives to time scales can usefully be shown in a conceptual manner. The "conceptual" approach (Wolfe & O'Connor 1986; Wolfe *et al* 1987) identifies three main aspects of monitoring. Firstly, compliance monitoring which attempts to ensure that activities are carried out to meet some legal requirements. Secondly, hypothesis testing or model verification, checks the validity of assumptions and predictions; and finally, trend monitoring, which identifies large-scale changes anticipated as a possible consequence of multiple activities.

A basic drawback in any monitoring programme is cost, which relates as much to time and expertise as it does to monetary expenditure. Therefore, careful planning is required and preferably a trial run. There have been a number of views on cost-effective sampling (Waters 1979; Resh & Price 1984), and, in particular, how to decide the number of sample units required and the appropriate apparatus. Within freshwater ecosystems, particularly stream systems, apparatus is used to remove an 'area' of the benthos, which is referred to as a "sampling unit", the size of which depends on the type of sampler utilized. It would require the total removal of the benthos to count all the benthic invertebrates present - not a feasible operation, so a statistical population is measured. The total area of the site under investigation is sometimes referred to as the 'population of sampling units' and it is from here that individual sample units are taken. Many freshwater ecologists adopt Elliott's usage (1977) of a series of 'sampling units', where the group of sampling units constitute the *sample.* Many statistical and specialist text books contain sections on sampling procedures and assessments of the number of samples required (Elliott 1977; Zar 1984; Krebs 1989). Random samples are always preferable as they give an unbiased estimate of the population, although because of the nature of freshwater habitats this often proves difficult to carry out.

Statistical procedures typically assume that samples are obtained in a random fashion. Green (1979) put forward a list of ten statistical principles for ecological research, which is added to by Allen (1984), and serve as a good guideline. A recent summary of contemporary field procedures by Voshell *et al* (1989) showed that the number of sample unit replicates used were mainly three to five, and the type of sampling device was generally an enclosed net (25%) and Surber sampler (43%). This is similar to the findings of Winterbourn (1985) where the Surber sampler (38%), hand net (28%), and box or cylinder samplers (22%) were the most common devices used in stream surveys.

In previous surveys of streams in the Ashdown Forest, in 1976 and 1984, Surber sampling was used (Townsend *et al* 1983; and Townsend *et al* 1987). It was found that five samples from each site yielded about 80% of all taxa, including many of the rarer ones. The Surber sampling device demarcates an area within which the substrate can be disturbed and animals washed downstream into a collecting pot, and is a 'quantitative' technique (Surber 1937, 1970). It is often used to investigate temporal and spatial changes in macroinvertebrate community structure. Usinger & Needham (1954) and Needham & Usinger (1956) found that sampling efficiency was affected by stream conditions and with different operators. With random placing of the frame, some stones may lie within the boundary and others outside of it, and it very much depends on personal judgement as to how this is handled, i.e. moving the frame until it is 'flush' with the substrate or moving it to encompass a large stone.

In addition to the Ashdown Forest stream sites I sampled another suite of stream sites. These are streams identified as being sensitive to acidification and incorporated into the UK Acid Waters Monitoring Network (UKAWMN), which was established in 1988 by the Department of the Environment following recommendations of the UK Acid Waters Review Group (Warren *et al* 1986). These sites will be referred to as either the UKAWMN or the DOE sites. The monitoring network consists of both lake and stream sites and aims to provide a minimum of ten years biological and chemical data to facilitate the assessment of trends in surface water acidity within the United Kingdom. The method of collecting benthic invertebrates agreed for the UKAWMN sites is to use kick samples with a pond net, a 'qualitative' method. Three, one minute samples from riffles are obtained by disturbing the substrate in front of the pond net which lies flush with the substrate and facing upstream. Since 1992 the number of kick samples has been increased from three to five, although the data since 1992 has not been used in the present analysis.

Several studies have compared samples taken using qualitative and quantitative methods (Hornig & Pollard 1978; Mackey *et al* 1984; Boulton 1985). The kick sample, using a standard pond net, has gained acceptance as a convenient, simple method and is widely used for biological monitoring. In several studies comparing Surber and kick sampling the general consensus seems to be that the kick samples are superior to the Surber for collecting species (Furse *et al* 1984; Storey *et al* 1991), although of course the aims of quantitative and qualitative sampling often differ. A quantitative sample in this context aims to provide an accurate estimate of the number of organisms in a given area, whereas the objective of qualitative samples is often to maximize the species list from a particular site. In recent years the kick sample has been the preferred method for collecting benthic samples by most UK water authorities for biomonitoring, and since the inception of the National River Authority (NRA), this is still the case.

As the Ashdown Forest surveys occurred in the autumn using Surber samplers, and the UKAWMN surveys take place in the spring using kick sampling, an attempt to account for the different season and method of sampling was necessary if it was to be possible to compare data from the different projects. Furse *et al* (1984) remarked that combining data from different seasons allowed for better grouping and prediction than using a single season.

The assessment of macroinvertebrates for the UKAWMN is carried out in this laboratory and so it was decided to compare the results of the Acid Waters Monitoring Network with those from previous and ongoing surveys of the Ashdown Forest streams. This had two objectives:

1) To assess community patterns in relation to environmental variables among both sets of sites combined (Chapter 6).

2) To assess community persistence (through time) in both sets of sites (Chapters 4 & 5).
In order to achieve these objectives some form of assessment of the compatibility of the two sampling methods was required, taking into account the different sampling seasons.

3.ii. METHODS.

Invertebrate sampling.

Five replicate Surber sample units (area 0.0625 m^2, mesh size 0.33mm) were taken from twenty-nine stream riffle sites in the Ashdown Forest in October 1989 and in March 1990. The substrate was removed to a depth of approximately 5 cm and invertebrates within the substrate were washed downstream into a collecting pot. At the same sites, three one-minute kick sample units were taken by moving upstream disturbing the substrate and using a square frame net with a mesh of 0.33 mm, according to DOE protocol. All material collected was preserved in the field using IMS (Industrial Methylated Spirits). The samples were hand sorted in the laboratory and the animals were counted and identified, to species where possible. For the DOE sites, collections were made in April and October 1990. The same methods were used, with the only difference being that samples were preserved in the field in Formaldehyde rather than in IMS.

Statistical analysis.

A data set of 58 paired samples (29 sites x two methods), was derived for each of the autumn and spring collections from the Ashdown Forest sites, and a data set of 24 paired samples (12 sites x two methods) for the spring and autumn collections from the DOE sites. Mean number of species and their percentage abundances were calculated for each site. Where required, data were transformed using $\log_{10}(x+1)$ and the suitability of the transformation was confirmed using Bartlett's test (Elliott 1977). For measures given as percentages, an arcsine transformation has been performed for any parametric statistics computed. (This is not a requirement where percentages range from 30% -70%).

Measurements of total abundance and species richness in Surber and kick samples were compared for all sites in the Ashdown Forest and the DOE sites. Correlations between Surber and kick samples, and between spring and autumn samples, were analysed using correlation coefficients. The correlation coefficient used here is the Spearman's Rank correlation coefficient, (Spearman 1904), which is calculated as

$$r_S = 1 - 6\sum D^2 / n(n^2 - 1)$$

Two types of Similarity Index are used, Jaccard's and Sorenson's (Sorenson 1948). Similarity coefficients were calculated between paired Surber and kick samples, using all taxa. The coefficients range from zero (no similarity) to 1 (complete similarity).

JACCARD $C_J = j/(a+b-j)$

SORENSON $C_S = 2j/(a+b)$
(or Czekanowski).

As there are no statistical probability distributions for similarity measures it was not possible to set confidence limits on these estimates of similarity and therefore not possible to assess error.

A t test for the differences between two diversity indices is used for both Ashdown Forest and UKAWMN sites. The Shannon index of diversity H', obtained from two samples, can be used to test the null hypothesis that the diversity of the two sampled populations are equal. Hutchinson (1970) proposes a test for this purpose. The equation for this is given below.

$$t = \frac{H'_1 - H'_2,}{S_{H'_1 + H'_2}}$$

where

$$S_{H'_1 + H'_2} = \sqrt{S^2 H'_1 + S^2 H'_2}$$

The DF associated with the proceeding *t* are approximated by :

$$\nu = \frac{(S^2 H' + S^2 H')^2}{\frac{(S^2 H'1)^2}{n_1} + \frac{(S^2 H'2)^2}{n_2}}$$

$S^2 H'$ is calculated using the tables of *fi* $\log^2$ *fi* provided by Lloyd, Zar & Karr (1968).

Classification with unweighted pair-groups method or (UPGMA), was performed for both Ashdown Forest and UKAWMN sites. It is a frequently used classification technique with a unique algorithm that appears to maximise the correlation between input dissimilarities (species by site matrix) and the output dissimilarities implied by the resulting dendogram (using the lowest level required to join any given sample pair in the dendogram). This is sometimes called the *cophenic correlation* (Sneath & Sokal 1973).

Hierarchical classification using polythetic-divisive methods have a theoretical advantage as all the information is used to make critical topmost divisions (Lambert *et al* 1973). These methods are recommended by Gauch (1982) as being effective and robust. Two-Way INdicator SPecies ANalysis, TWINSPAN, is an iterative technique. Data are first ordinated by reciprocal averaging. Those species at the extremes are emphasized to polarise the samples, and the samples are then divided into two clusters by breaking the ordination axis near its middle. This is repeated on two sample subsets to give four clusters, and so on. A species classification is also produced, but with this data set we are interested in the site classifications, and whether or not the different sampling methods are grouped together for each site. In Table 3.1 sampling occasions are given for both suites of sites.

Table 3.1 A table of sampling occasions is given below, + indicates when a sample was taken.

YEAR	SEASON	ASHDOWN FOREST		UKAWMN	
		Surber	Kick	Surber	Kick
1976	Spring				
	Autumn	+			
1984	Spring				
	Autumn	+			
1988	Spring				+
	Autumn				+
1989	Spring			+	+
	Autumn	+	+		
1990	Spring	+	+	+	+
	Autumn			+	+
1991	Spring			+	+
	Autumn				

3.iii. RESULTS.

Numbers.

The Log_{10} of the total numbers of individuals, and the total number of species collected in autumn and spring samples are given for each of the Ashdown Forest stream sites in Fig 3.1. Very little difference was found between sampling methods for the total number of individuals and, although there are vast differences between sites, there is broad agreement between Surber and kick samples. With regard to number of species, Surber samples generally collected more than kick sampling. Overall, autumn samples contained the greater number of individuals. The UKAWMN stream sites also illustrate broad agreement for total numbers of individuals, but there are some sites where there are large differences between numbers of species obtained in Surber and kick samples (Fig 3.2). For instance, the autumn collections from Beagh's Burn show that kick samples contained the greater number of species but there were more species in Surber samples in spring. Spring samples generally had the greater number of individuals and more species than autumn samples.

For the Ashdown Forest sites in autumn 1989, mean numbers of individuals per Surber and kick sample, and mean numbers of species collected in Surber and kick samples are plotted in Fig. 3.3. There is a significant correlation between the two methods, although, for the majority of stream sites, more individuals and species were collected in Surber samples.

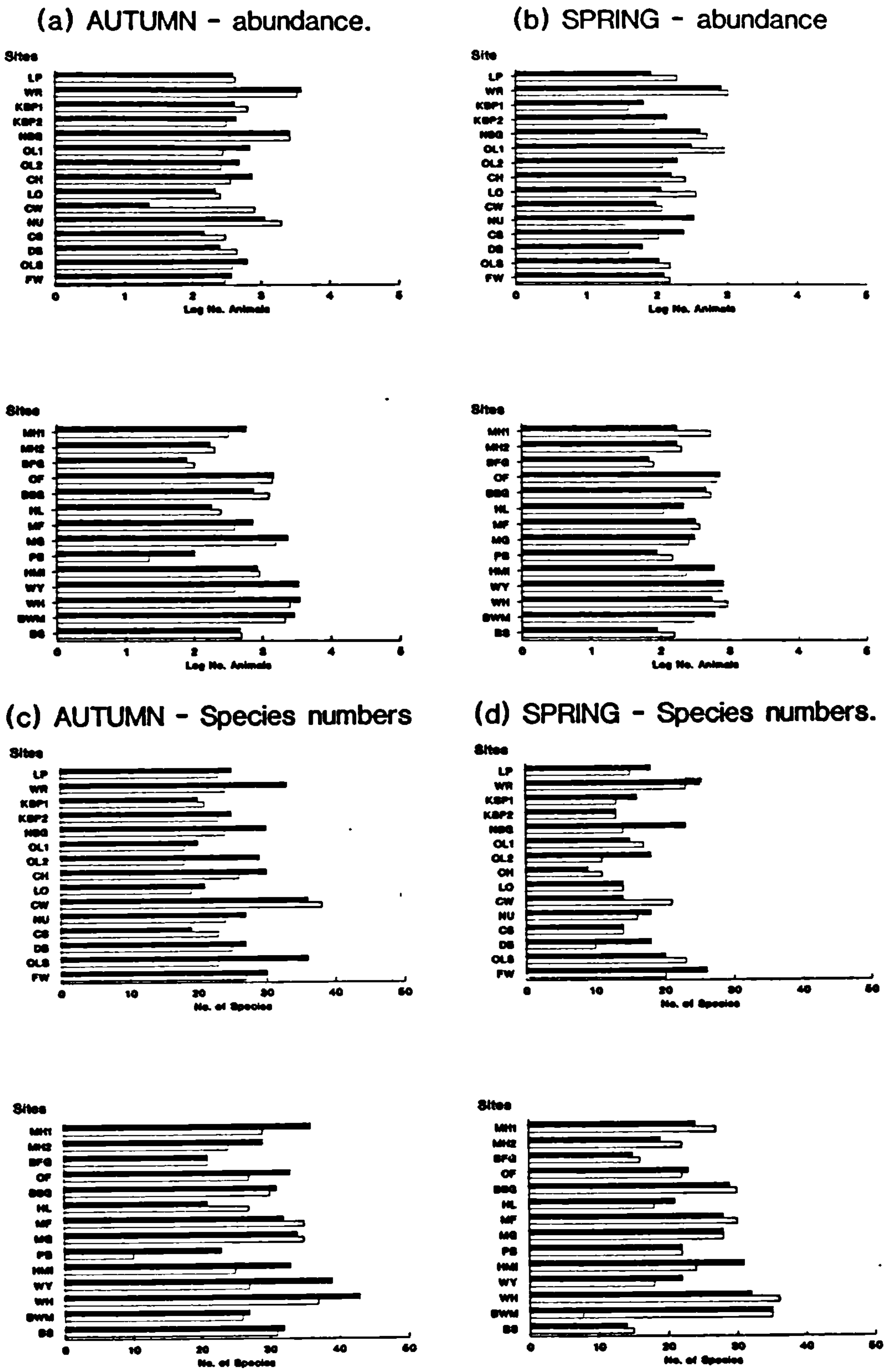


Fig 3.1: A comparison of Surber (closed bars) and kick sampling (open bars) in the Ashdown Forest in Autumn 1989 and Spring 1990 : (a) & (b) shows the Log_{10} number of animals per sample in Autumn and Spring, respectively, and (c) & (d) shows the number of taxa per sample in Autumn and Spring, respectively.

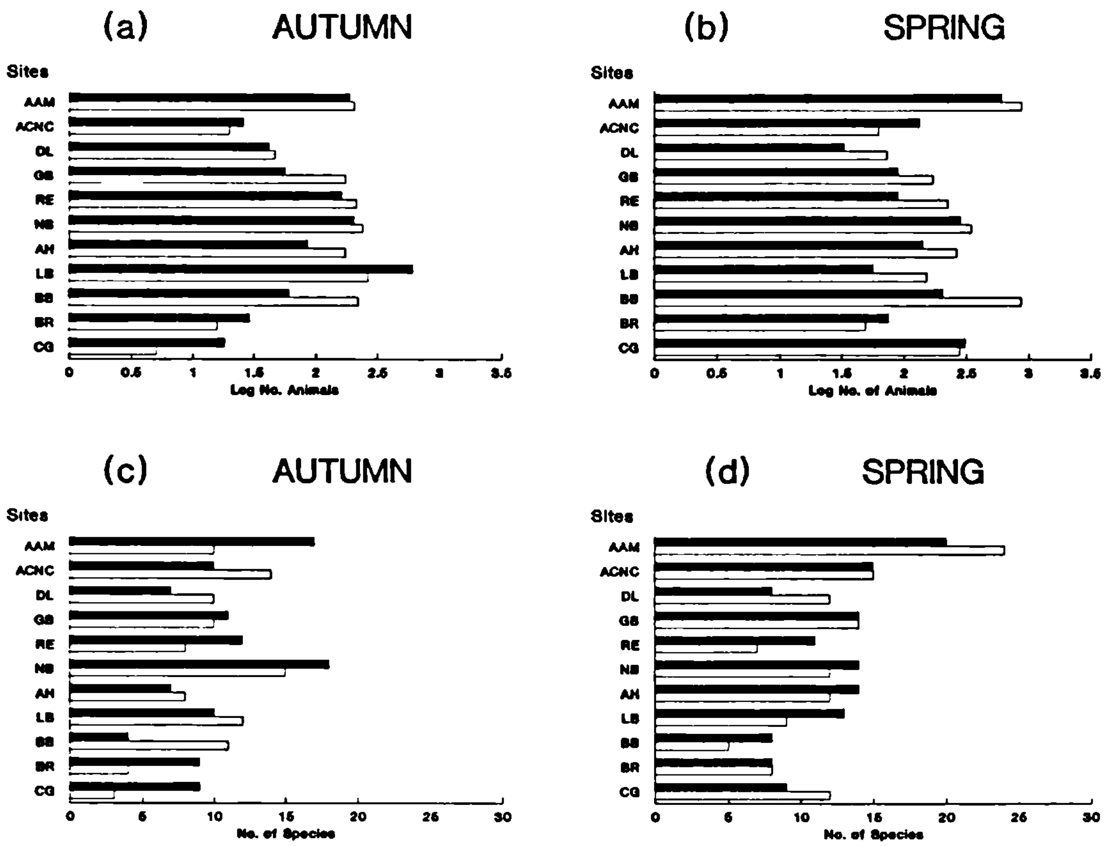


Fig 3.2 A comparison of Surber (closed bars) and kick sampling (open bars) in the UKAWMN sites in Autumn & Spring 1990: (a) & (b) shows the Log_{10} number of animals per sample in autumn and spring ,respectively, and (c) & (d) shows the number of taxa per sample in Autumn & Spring, respectively.

In Fig. 3.4. the mean number of animals and the mean number of species collected from the Ashdown Forest stream sites in the spring 1990 are plotted. Again, both are highly correlated with correlation coefficients of 0.840 for the number of individuals and 0.812 for the number of species. Spring samples had a coefficient of $r = 0.50$ for the mean number of individuals and $r = 0.068$ (not significant) for the mean number of species. For the autumn, the figures were $r = 0.197$ (not significant) for the mean number of individuals and $r = -0.037$ (not significant) for the mean number of species. Some of the UKAWMN stream sites had very low correlation coefficients and have not been plotted. It is possible that this was due to either Surber or kick sampling not being suitable for use on the substrate type of particular streams.

The data for subsets of the community can also be examined. Scatter plots for the Ashdown Forest stream sites for Trichoptera, for autumn 1989 and spring 1990, are presented in Fig. 3.5. Greater numbers of Trichoptera were collected in Surber samples than in kick samples for both autumn and spring. Figure 3.6 gives the scatter plots for Trichoptera in Surber and kick samples, for spring and autumn 1990, for the UKAWMN stream sites. There was little difference overall in the numbers collected in the two seasons by the two methods. The other group of macroinvertebrates examined are Plecoptera. Data from the Ashdown stream sites are presented in Fig. 3.7, where scatter plots of Surber and kick samples for the autumn 1989 and spring 1990 are given. Here, there is little difference between the numbers of Plecoptera collected by the two methods in the autumn, but a greater number were collected in kick samples in the spring. In Figure 3.8. scatter plots of the Surber and kick samples from the UKAWMN stream sites are presented for the spring and autumn 1990. In all but two sites, there were greater numbers of Plecoptera collected in kick samples in the autumn, and for all but three stream sites in the spring.

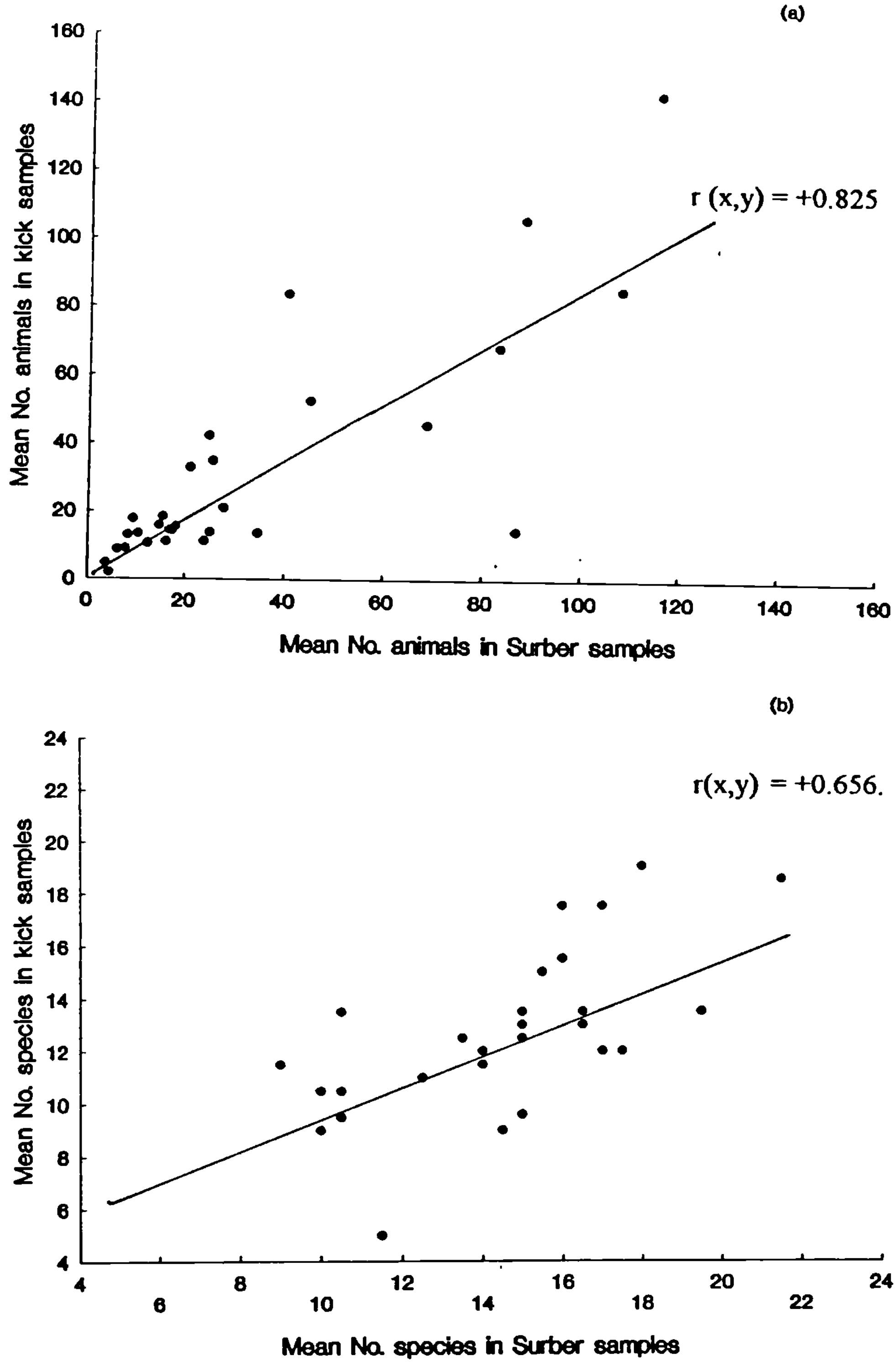


Fig 3.3. Ashdown Forest stream sites. Autumn 1989. Mean number of individuals and mean number of species collected in Surber and kick samples are plotted in (a) & (b) respectively. For (a) r (x,y) = + 0.825, and for (b) = + 0.656.

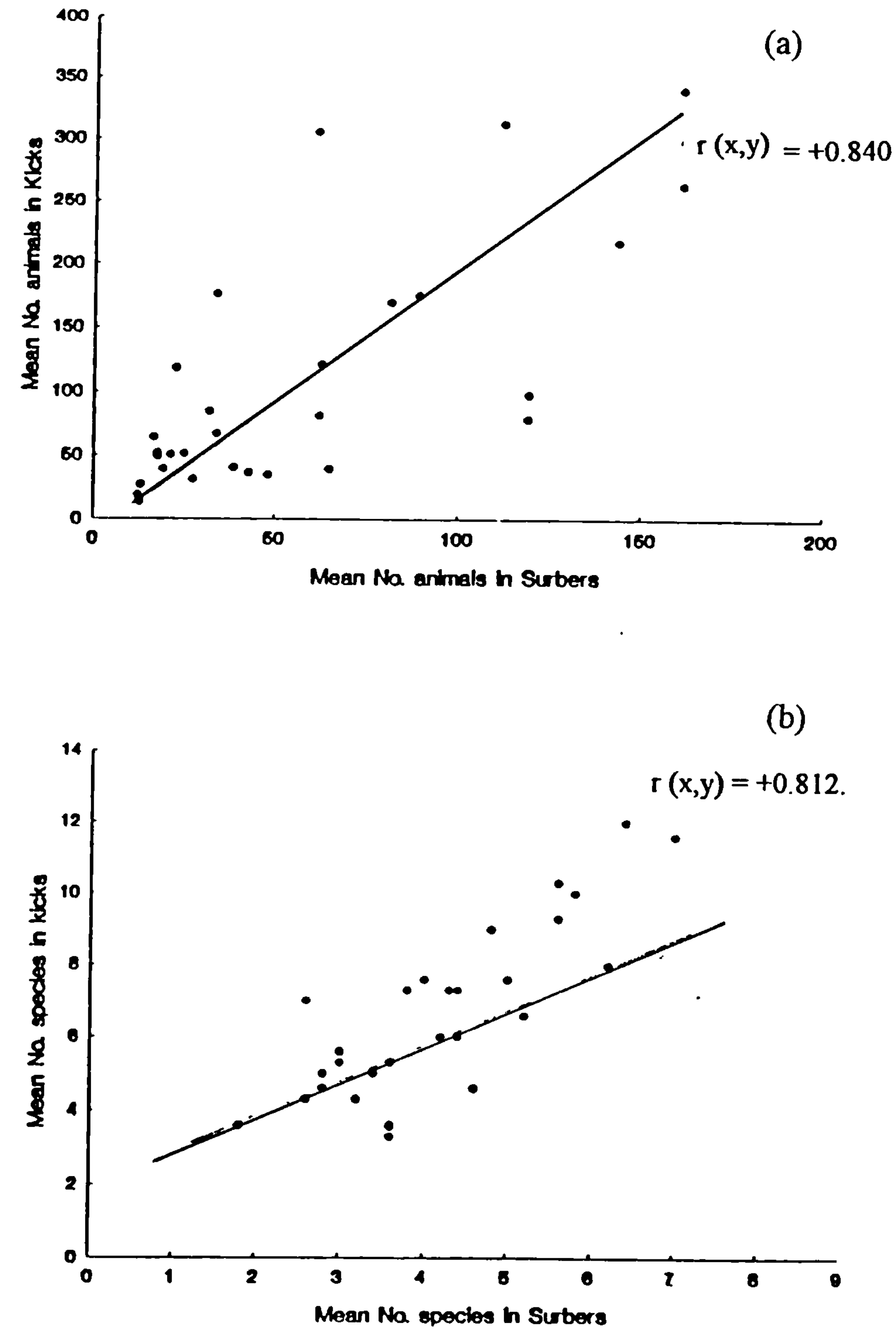
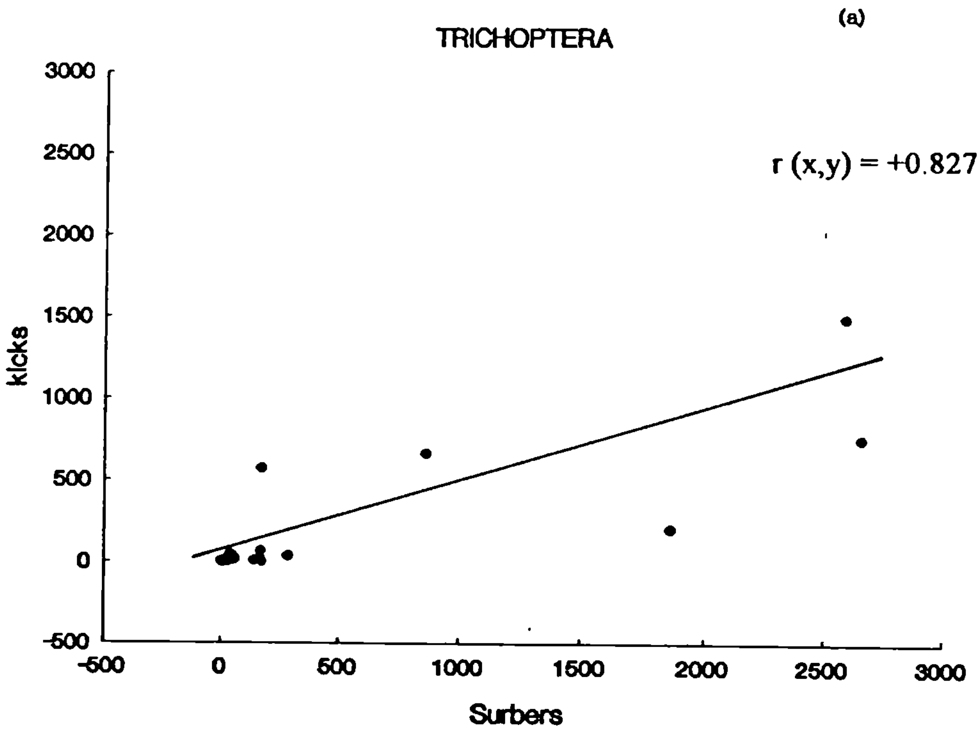


Fig 3.4 Ashdown Forest stream sites. Spring 1990. Mean number of individuals and mean number of species collected in Surber & kick samples are plotted in (a) & (b), respectively. For (a) r (x,y) = + 0.840 and for (b) = + 0.812.



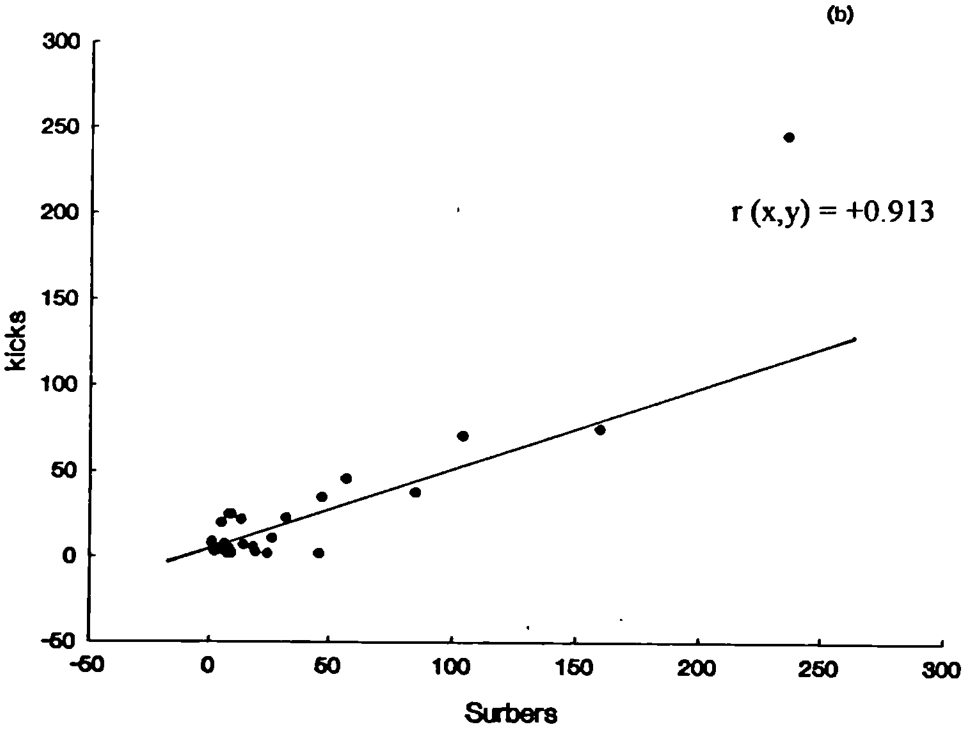
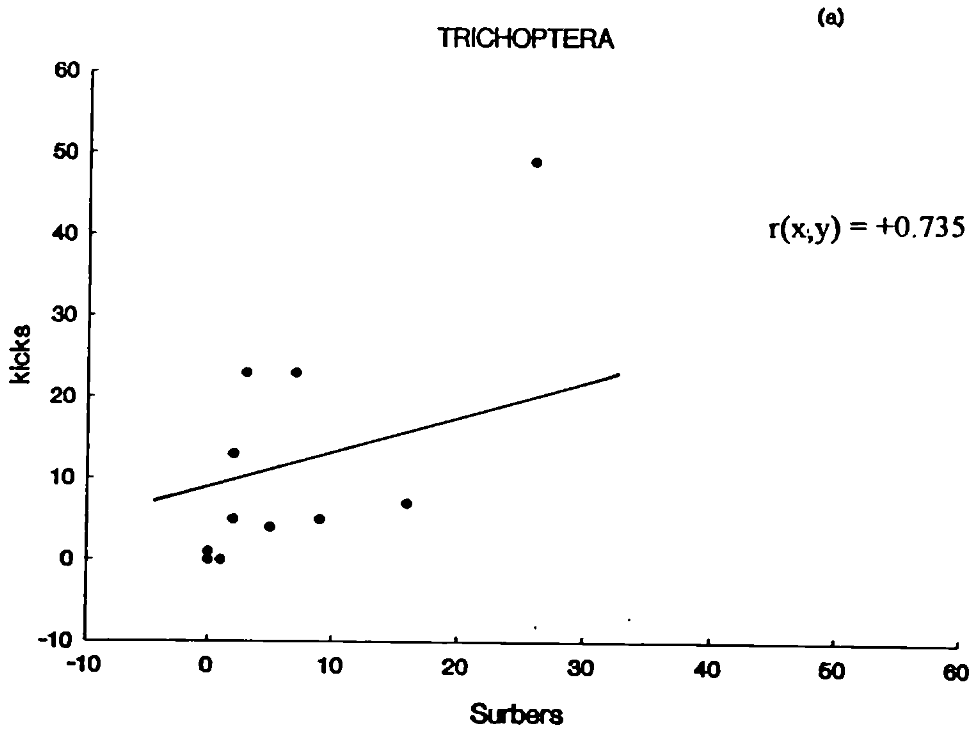


Fig 3.5. Ashdown forest stream sites. Autumn 1989. Number of trichoptera collected in Surber and kick samples are plotted in (a), and for Spring 1990 in (b). For (a) r (x,y) = + 0.827 and (b) = + 0.913.



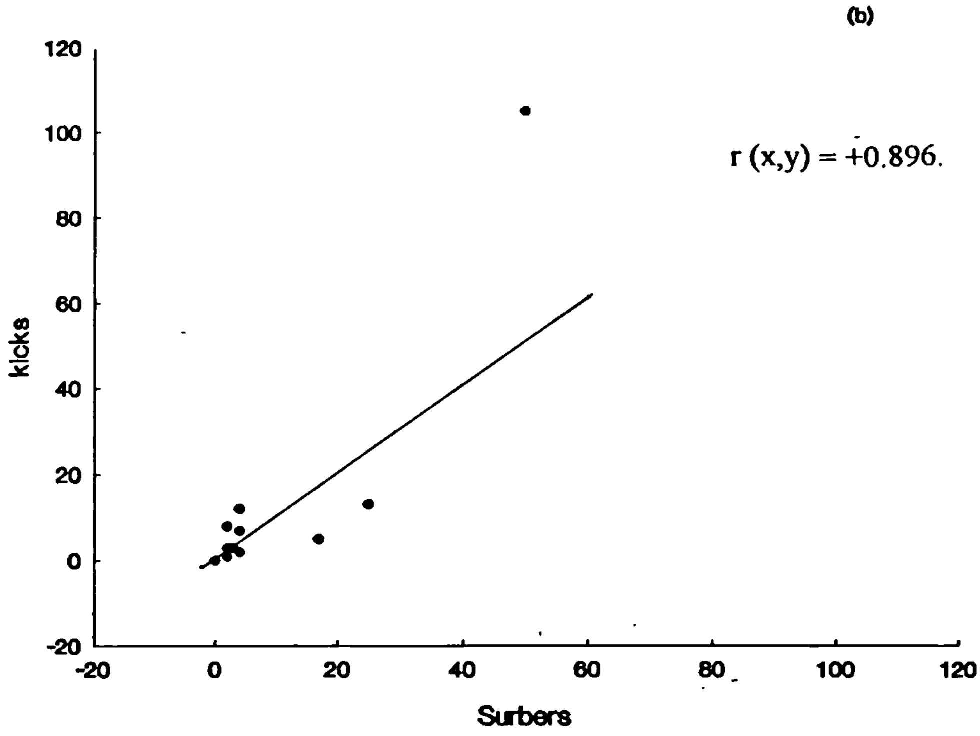


Fig 3.6. UKAWMN stream sites. Spring & Autumn 1990. Numbers of Trichoptera collected in Surber and kick samples are plotted in (a) and (b), respectively. For (a) r (x,y) = + 0.735 and (b) = + 0.896.

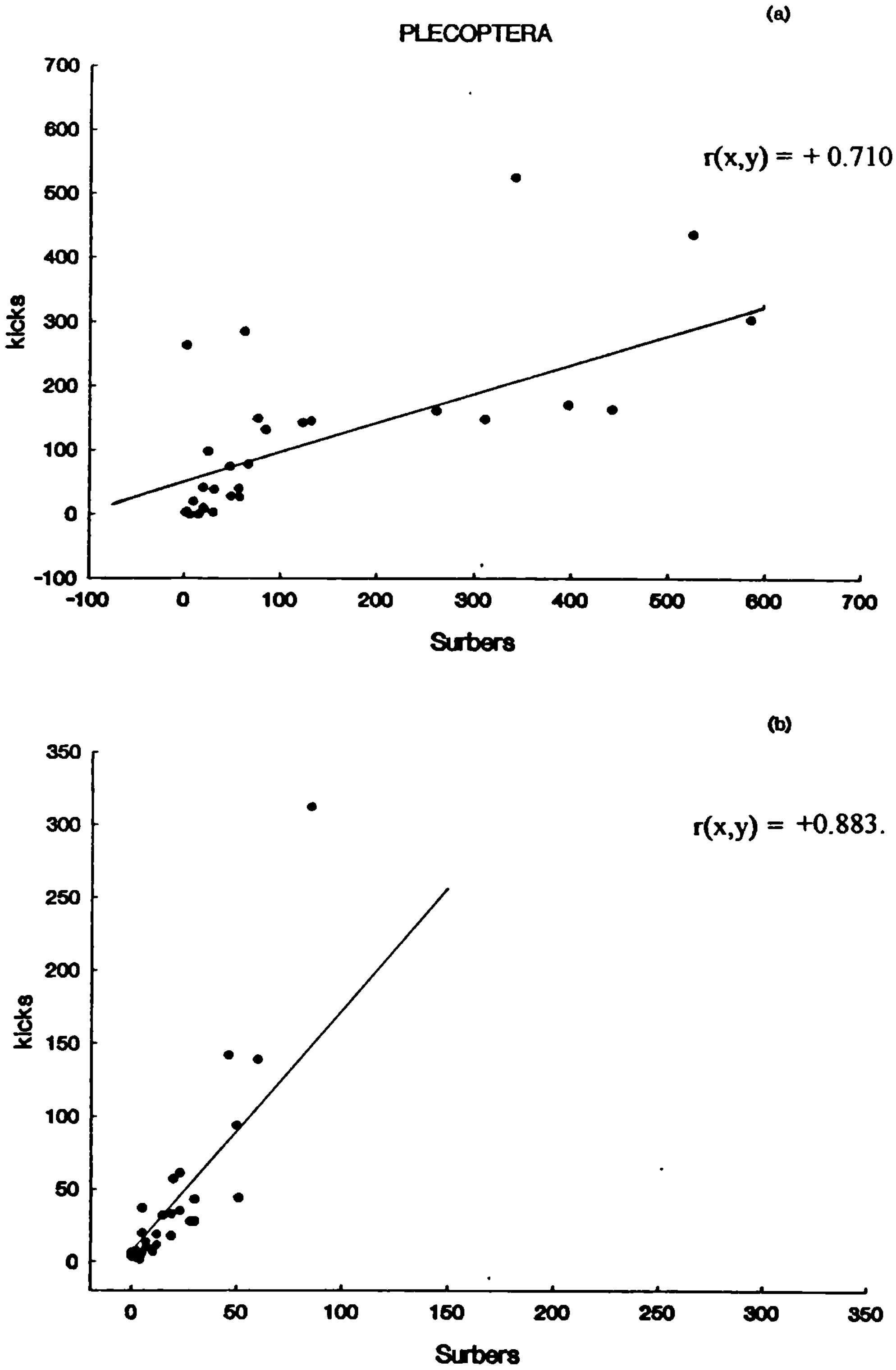


Fig 3.7. Ashdown Forest stream sites. Autumn 1989 and Spring 1990. Plecoptera collected in Surber and kick samples are plotted for autumn (a) & spring (b). For (a) r (x,y) = + 0.710 and for (b) = +0.883.

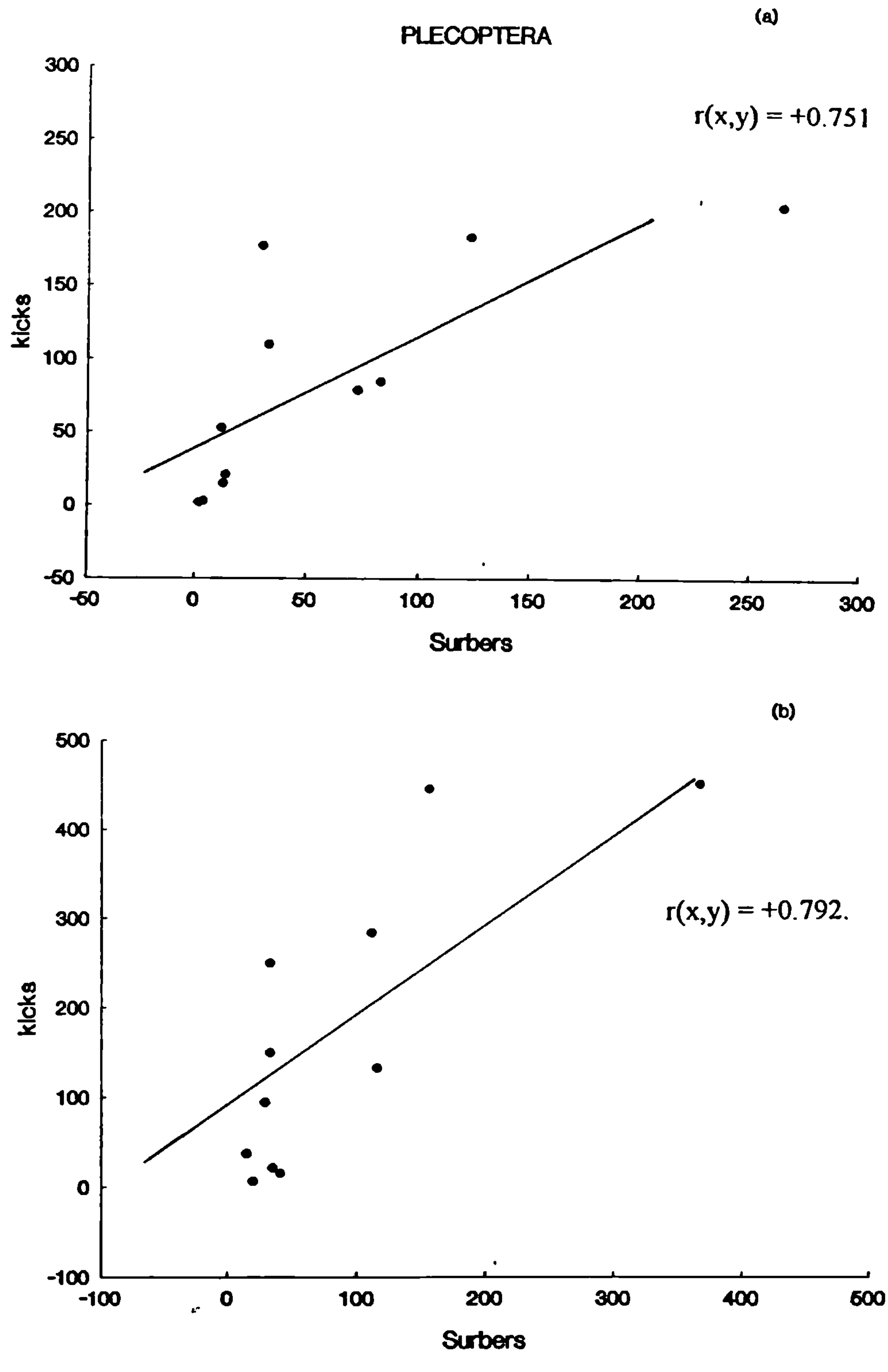


Fig 3.8. UKAWMN stream sites. Spring & Autumn 1990. Number of Plecoptera collected in Surber and kick samples are plotted for spring (a) and autumn (b) respectively. For (a) r (x,y) = + 0.751 and for (b) r (x,y) = + 0.792.

3.iv. Species diversity.

t tests for differences between the Shannon diversity indices calculated from the samples taken by the two methods for the Ashdown Forest stream sites are given in Table 3.2. The null hypothesis is that there are no significant differences between the diversity indices calculated from Surber and kick samples. For the Ashdown Forest the null hypothesis was rejected for 10 out of 29 sites but there is no obvious factor linking them. Table 3.3 gives the results of the *t* test for the difference between two diversity indices for the UKAWMN stream sites. Of the eleven sites only two reject the null hypothesis, these are Beagh's Burn and the River Etherow. (Old Lodge1 is included with the the Ashdown suite of sites in Table 3.2).

3.v. Rank abundance.

Spearman's rank correlation coefficient for the rank abundance of species in the two samples (Surbers and kicks), from each site, were calculated for spring and autumn, for both the Ashdown Forest streams and the UKAWMN stream sites. Table 3.4 gives the Spearman's *r* for both seasons and both suites of stream sites. Figure 3.9 gives frequency distributions for Spearman's *r* for both the Ashdown Forest streams and the UKAWMN sites, for spring and autumn. All but one site (number 4 in the Ashdown Forest, KBP2) has a significant rank correlation and this site is indicated with an asterisk.

t Test for the difference between two diversity indices - Ashdown sites.

$$H_1 = \frac{n \log n - \sum fi \log fi}{n}$$

$$S_2 H_1 = \frac{\sum fi \log^2 fi - (\sum fi \log fi)\, 2/n}{n}$$

$$t = \frac{H_1 - H_2}{S_2 H_1 - H_2} \quad \text{Where } S_2 H_1 - H_2 = \sqrt{S_2 H_1 + S_2 H_2}$$

H_0: There is no difference between the diversities of the sample populations collected with Surbers and with kick samples.

Table 3.2: Results of *t* Tests between two diversity indices. Ashdown sites.

SITE	t	t 0.05 (2)	H_0
LP	-3.8	1.96	Accept
WR	1.4	1.70	Accept
KBP1	-1.7	1.96	Accept
KBP2	-0.8	12.7	Accept
NBG	12.6	1.96	Reject
OL1	0.2	1.96	Accept
OL2	-7.4	1.97	Accept
CH	-12.4	1.96	Accept
LO	-2.6	1.97	Accept
CW	2.4	1.90	Reject
NU	18.6	1.96	Reject
CS	-1.0	1.96	Accept
DB	7.7	2.00	Reject
OLS	7.2	1.96	Reject
FW	-13.1	1.98	Accept
MH1	1.7	1.96	Accept
MH2	4.9	2.00	Reject
BFG	-1.5	2.03	Accept
OF	3.6	2.01	Reject
BBG	8.0	1.99	Reject
HL	-6.9	2.03	Accept
MF	-8.5	1.96	Accept
MG	-5.4	1.96	Accept
PB	8.7	2.10	Reject
HMI	-1.4	2.00	Accept
WY	-0.4	2.02	Accept
WH	7.6	1.96	Reject
BWM	-14.5	1.96	Accept
BS	1.9	1.99	Accept.

t Test for the difference between two diversity indices - UKAWMN sites.

$$H_1 = \frac{n \log n - \sum fi \log fi}{n}$$

$$S_2 H_1 = \frac{\sum fi \log^2 fi - (\sum fi \log fi)\, 2/n}{n}$$

$$t = \frac{H_1 - H_2}{S_2 H_1 - H_2} \quad Where\ S_2 H_1 - H_2 \quad \sqrt{S_2 H_1 + S_2 H_2}$$

H_0: There is no difference between the diversities of the sample populations collected with Surbers and with kick samples.

Table 3.3: Results of *t* Tests between two diversity indices. UKAWMN sites.

SITE	t	t 0.05 (2)	H_0
Alt a Mharcaidh	-3.78	1.96	Accept
Alt Coire Nan Con	0.35	2.16	Accept
Green Burn	0.58	1.96	Accept
Dargall Lane	-3.77	2.16	Accept
Bencrom River	-0.53	2.12	Accept
Beagh's Burn	6.14	2.10	Reject
Coney Glen	-6.31	2.10	Accept
River Etherow	2.31	2.04	Reject
Narrator Brook	-8.86	12.7	Accept
Afon Hafren	-0.43	2.5	Accept
Llyn Brianne	1.84	2.06	Accept

Table 3. 4: Table of Spearman's rank correlation coefficients for the Ashdown Forest stream sites and the UKAWMN sites - autumn and spring. All coefficients are significant except for sites indicated by *.

ASHDOWN FOREST			UKAWMN		
SITE	Spearman's *r*, Autumn	Spearman's *r*, Spring.	SITE	Spearman's *r* Autumn	Spearman's *r* Spring
LP	0.853	0.810	AAM	0.698	0.663
WR	0.745	0.662	ACC	0.785	0.697
KBP1	0.823	0.811	GB	0.896	0.821
*KBP2	0.393	0.423	DL	0.664	0.622
NBG	0.720	0.704	BR	0.789	0.862
OL1	0.885	0.637	BB	0.803	0.856
OL2	0.711	0.685	CG	0.785	0.806
CH	0.816	0.744	RE	0.668	0.724
LO	0.819	0.822	NB	0.785	0.827
CW	0.745	0.600	AH	0.599	0.604
NU	0.961	0.756	LB	0.913	0.926
CS	0.783	0.721			
DB	0.735	0.632			
OLS	0.795	0.569			
FW	0.796	0.612			
MH2	0.795	0.724			
BFG	0.861	0.711			
OF	0.657	0.489			
BBG	0.927	0.826			
HL	0.869	0.741			
MF	0.904	0.816			
MG	0.821	0.724			
PB	0.919	0.823			
HMI	0.834	0.694			
WY	0.884	0.723			
WH	0.779	0.631			
BWM	0.916	0.815			
BS	0.942	0.836			

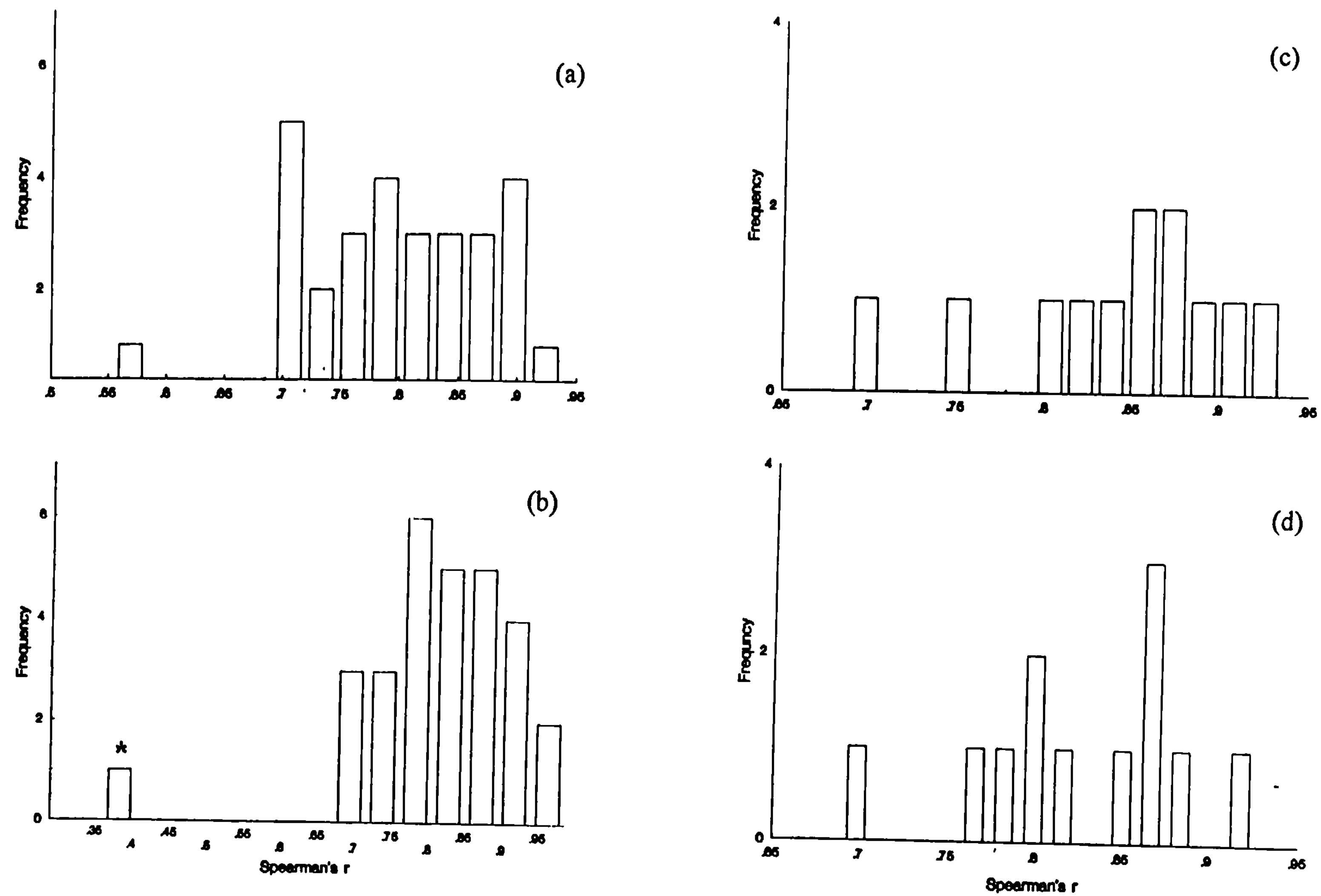


Fig. 3.9: Spearman's rank correlation coefficients for rank abundance of species in Surber and kick samples for Ashdown Forest sites Autumn (a) and Spring (b) and for the UKAWMN stream sites, Autumn (c) and Spring (d). Apart from Kidbrook Park, which is marked (*), all sites have a significant Spearman's *r*

3.vi. Community patterns.

Similarity indices between Surber and kick samples for the Ashdown Forest have been calculated and are presented in Table 3.5. Both Jaccard's and Sorenson's index have been calculated for the spring and autumn data. Sorenson's index has been recommended as a good binary index of community similarity (Smith 1986). For the UKAWMN stream sites the similarity indices are found in Table 3.6. For all sites the similarity index is high.

In Figure 3.10. frequency distributions for Sorenson's index (between Surber and kick samples) are given. The figure contains graphs for spring and autumn and for the Ashdown suite of sites and the UKAWMN stream sites. Only one site does not have a significant index, and this is PB (Pooh's Bridge) in the Ashdown Forest autumn sample, (a in Fig).

Classification of sites by cluster analysis allows for a visual or graphical method of examining and interpreting levels of affinities between groups. That is, where there is a collection of samples, classification allows one to see which are the most closely related. Similarity indices can be used for this, but here I have also used TWINSPAN to classify the Ashdown Forest and UKAWMN stream sites, using Surber and kick samples. In Fig. 3.11, the Ashdown Forest spring data is presented in a dendrogram at the top of the page giving results for spring only (autumn is virtually identical). The lower case letter s and k refer to Surber and Kick respectively. Ashdown Forest sites are classified to two levels. For the UKAWMN sites, all the sites are grouped together as far as different sampling methods go, until the final division when Coney Glen, Bencrom River and Old Lodge separate Surber and kick samples.

Table 3.5: Similarity indices for Ashdown sites between Surber and kick samples taken in the Autumn (A) and Spring (S).

ASHDOWN FOREST - SIMILARITY INDICES - AUTUMN AND SPRING.

SITES	JACCARD'S		SORENSON'S	
	A	S	A	S
LP	0.66	0.6	0.79	0.75
WR	0.63	0.66	0.77	0.79
KBP1	0.64	0.38	0.78	0.55
KBP2	0.81	0.53	0.89	0.69
NBG	0.74	0.61	0.85	0.65
OL1	0.73	0.60	0.84	0.75
OL2	0.50	0.38	0.67	0.55
CH	0.87	0.43	0.93	0.60
LO	0.67	0.50	0.67	0.67
CW	0.89	0.80	0.95	0.63
NU	0.59	0.48	0.75	0.65
CS	0.68	0.55	0.81	0.71
DB	0.73	0.55	0.85	0.71
OLS	0.54	0.60	0.66	0.74
FW	0.84	0.77	0.91	0.87
MH1	0.63	0.70	0.77	0.82
MH2	0.71	0.71	0.83	0.83
BFG	0.50	0.55	0.67	0.71
OF	0.71	0.87	0.83	0.93
BBG	0.79	0.90	0.88	0.95
HL	0.60	0.56	0.75	0.72
MF	0.68	0.76	0.81	0.86
MG	0.92	0.60	0.96	0.75
PB	0.32	0.63	0.48	0.73
HMI	0.74	0.72	0.86	0.84
WY	0.62	0.70	0.73	0.82
WH	0.78	0.80	0.87	0.89
BWM	0.63	0.67	0.76	0.80
BS	0.80	0.61	0.89	0.56

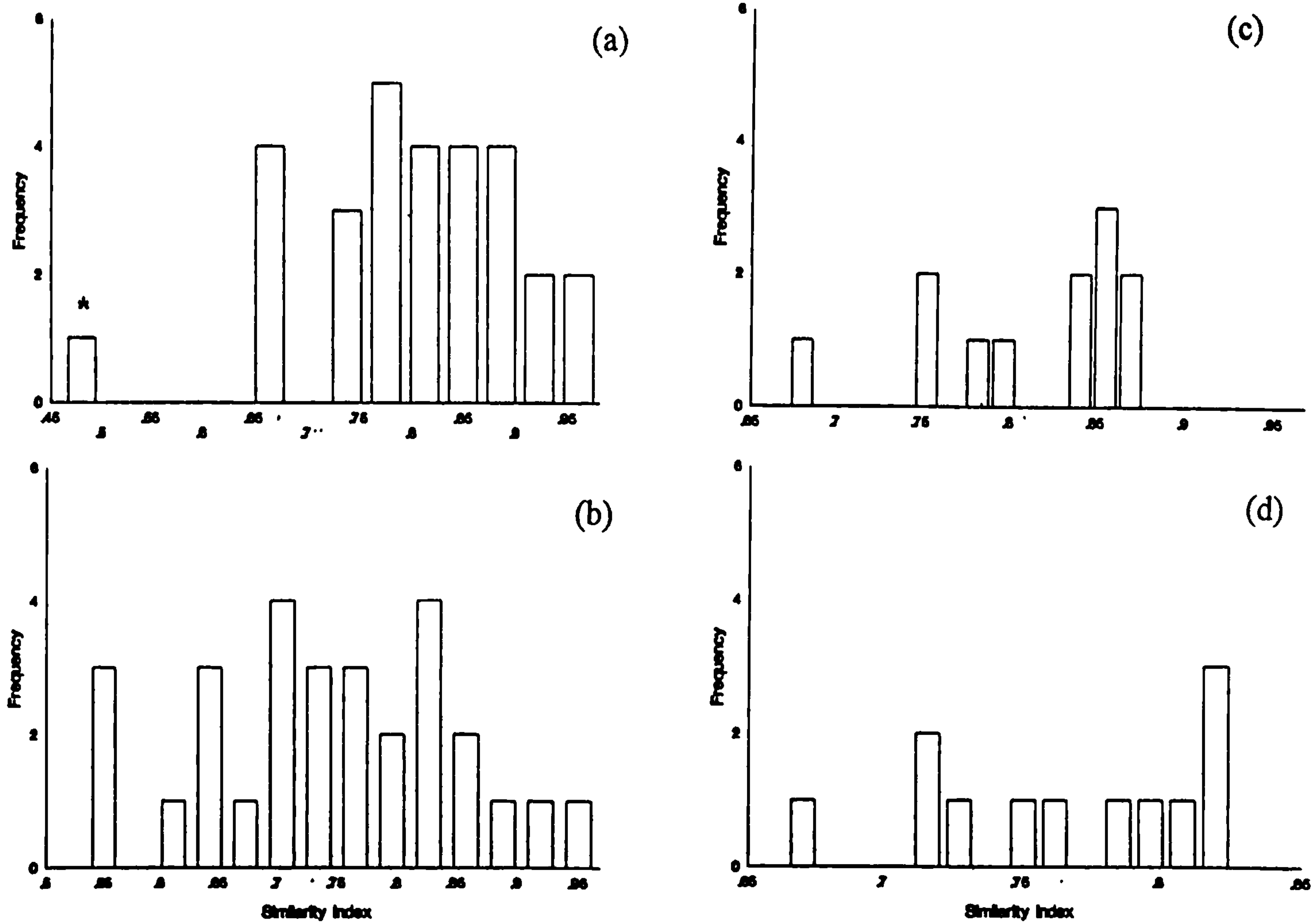


Fig. 3.10: Ashdown Forest stream sites given in (a) & (b). Frequency distributions for Sorenson's Similarity Index for Surber and kick samples are presented for Autumn 1989 (a) and Spring 1990 (b).
UKAWMN stream sites. Frequency distributions for Sorenson's Similarity Index between Surber and kick samples are given for Spring 1990 (c) and Autumn (d). Only one site does not have a significant result (a), and is highlighted with a symbol *.

Table 3.6: Similarity indices for UKAWMN sites between Surber and kick samples taken in Autumn (A) and Spring (S).

UKAWMN SITES - SIMILARITY INDICES - AUTUMN AND SPRING.

SITES	**JACCARD'S**		**SORENSON'S**	
	A	**S**	**A**	**S**
Alt a Mharcaidh	0.52	0.55	0.68	0.67
Alt Coire nan Con	0.74	0.68	0.85	0.81
Dargall Lane	0.68	0.66	0.76	0.73
Green Burn	0.62	0.60	0.78	0.72
R. Etherow	0.73	0.71	0.86	0.80
Old Lodge	0.73	0.60	0.84	0.75
Narrator Brook	0.79	0.68	0.87	0.82
Beagh's Burn	0.69	0.61	0.79	0.76
Bencrom River	0.69	0.61	0.75	0.72
Coney Glen	0.72	0.70	0.85	0.82
Afon Hafren	0.67	0.68	0.87	0.82
Llyn Brianne	0.74	0.71	0.84	0.79

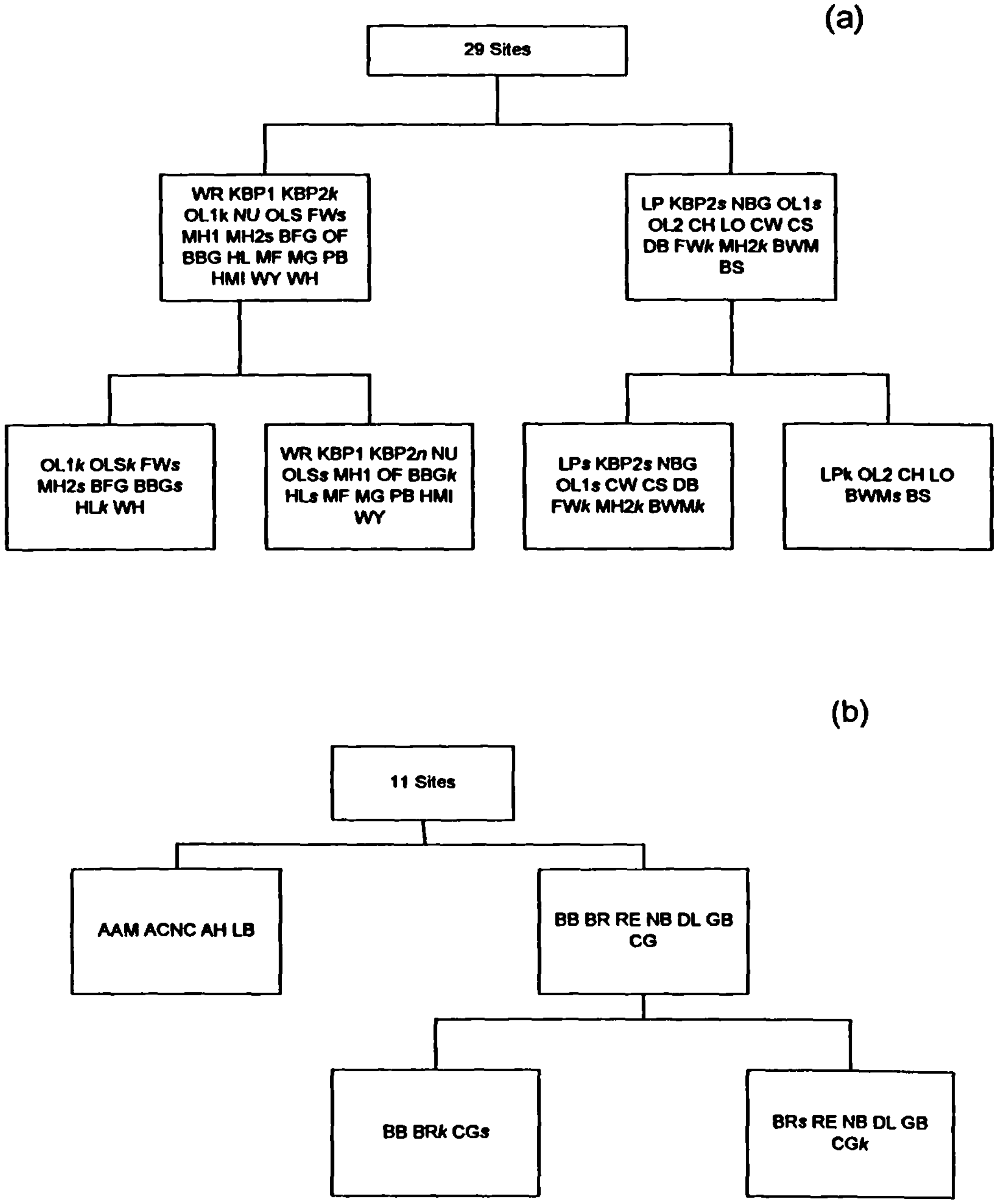


Fig 3.11
Classification, using TWINSPAN, for Ashdown Forest stream sites is given in (a). Surber and kick samples were classified together and divisions are given to two levels. Where site numbers are listed alone, this indicates Surber and kick samples are classified together, only where an italic lower case letter is given is there a separation. In (b) the UKAWMN stream sites are classified using TWINSPAN. Here all sites are classified together as Surber and kick samples until the final division, where Coney Glen (CG), Bencrom River (BR) and Old Lodge (OL) separate out. For both Ashdown and UKAWMN sites, classification has been performed using spring data (1990). Autumn data gives very similar results.

3.vii. DISCUSSION.

Autumn and spring are traditionally the times for collecting benthic invertebrates, because the summer months encompass the adult flight period of many aquatic insects. As the Ashdown Forest streams have been sampled in the autumn and the UKAWMN sites in the spring a seasonal comparison was necessary.

One would expect that kick sampling would give a greater abundance of macroinvertebrates because of the larger surface area of the stream bed covered by kick sampling. This was not the case for the Ashdown Forest stream sites. Autumn samples had a greater number of individuals collected in each Surber sample, whereas there were marginally more individuals collected in each kick sample in spring. With regard to species richness, Surber samples collected a greater number of species in the Ashdown Forest streams for both the autumn and spring. The kick samples appeared to be biased towards the collection of abundant taxa but not representative of low occurrence taxa. In the UKAWMN stream sites there were more individuals in kick samples in both seasons and a greater number of species in the spring kick samples but more in the Surbers in the autumn. This is similar to the results obtained in a study by Storey *et al* (1991) which took place in Australia. There are several possible reasons for this, such as an early spring emergence or recent disturbance events. For individual samples there were no discernible patterns. There was little difference between sampling methods. There were marked differences in the results between the two suites of sites, however, with Surber samples the better method of collection for the Ashdown Forest and kick sampling for the UKAWMN. In general, the autumn Surber samples collected more Trichoptera and Coleoptera, and more Plecoptera in the spring as percentage abundance. In contrast, kick samples collected more Plecoptera in the autumn with no discernible differences in the spring.

Obviously, if a particular species or taxon is being monitored as a sensitive bio-indicator, then the method of collection is going to be important. Past investigations have found kick sampling to be superior for collecting most species as compared to Surber sampling (Hornig & Pollard 1978). However, it was noted by Mackey *et al* (1984) that this was not always the case, and suggested that substratum differences may have a bearing on the efficiency of the sampling method - this remains an area open for investigation. Hornig & Pollard (1978) proposed that the kick technique would sample the more easily dislodged and highly mobile taxa while the Surber method, being more intensive, would collect cryptic and closely adherent taxa. This may be the case in this study.

It is perhaps a cause for concern that kick samples do not appear to detect low-occurrence taxa, particularly as this is the preferred method for environmental impact assessments, given that part of such assessments are the detection of rare species. With regard to the UKAWMN survey, kick samples collected more species in the spring (when the survey is carried out), although Surber samples had more species in the autumn, and for both seasons for the Ashdown Forest stream sites. A precautionary measure may be initially to use both methods, particularly in areas not previously sampled, to ensure the initial detection of rare taxa.

For the majority of sites, both methods produced similar species lists, as was demonstrated by the relatively high similarity indices. High similarity was recorded for both the spring and autumn, indicating that seasonality in the benthic invertebrate fauna of streams in different regions did not affect the ability of the two methods to produce similar species lists. However, seasonal changes in stream discharge may influence the ability of the two methods to produce comparable data on community composition. This was demonstrated by the highly variable data for the autumn samples for the UKAWMN sites, particularly at Coney Glen which was close to flooding at time of collection. Both methods are flow dependent and reduced discharge may affect sampling efficiency. There are, of course, flow independent sampling devices (Boulton 1985), but the increased accuracy for routine monitoring may not justify the extra expense. There are no streams within the UKAWMN suite of sites which are consistently low in species numbers or abundance for both seasons (taking into account that acid streams do not boast large species lists). For the Ashdown Forest streams, generally the circum-neutral streams had the higher number of species, but there was no discernible difference between acid and circum-neutral streams for numbers of animals. In fact, Pooh's Bridge, a circum-neutral site, had low abundance of animals in both seasons and this was particularly obvious in the autumn. This was detected by the similarity indices. Sorenson's index for the autumn was 0.48 for Pooh's Bridge, and for the spring was 0.55 for Kidbrook Park 2 . Otherwise the similarity indices for all other sites, both in the Ashdown Forest and the UKAWMN, were high.

Mackey *et al* (1984) reported that kick samples are sensitive to operator differences, and Furse *et al* (1981) noted a significant difference between operators with respect to the number of families and species taken. However, they observed 'strong site faithfulness' when data were analysed by clustering and ordination procedures. High correlations, high similarity and cluster analysis give a good enough fit to allow for the use of the data collected by the two sampling methods in subsequent multivariate analysis, using percentage abundance or presence / absence data. This is relevant for the work described in Chapter 6, where the Ashdown Forest and UKAWMN stream sites are analysed together.

We have seen that both methods have their advantages and disadvantages. Surber samples cannot be obtained from streams where the water levels are high but is a quantitative method for collecting benthic invertebrates. The final design of a sampling programme is often the compromise between statistical accuracy and labour (Elliott 1977). It is recognised that the kick sampling method provides a substantial saving in costs over Surber sampling, with a minimal loss of information. Surber sampling is appropriate for the Ashdown Forest stream sites. These have a fairly uniform substrate and are only rarely difficult to sample. That is not to say that they have all-year round low discharge, as water levels can occasionally make sampling difficult. With regard to the UKAWMN sites, these streams have variable substrates, from fine gravel and cobbles to large boulders. The flow regimes are also more variable, making sampling sometimes hazardous.

CHAPTER 4.

COMMUNITY PERSISTENCE IN SOME SOUTHERN ENGLISH STREAMS.

4.i .INTRODUCTION

A survey of benthic macroinvertebrates in stony riffles at thirty-four stream sites was undertaken in October 1976 in an area known as the Ashdown Forest in East Sussex (Townsend *et al* 1983). The data showed that several physicochemical factors, mainly stream pH, were related to the structure of the benthic communities. Summer temperatures and stream discharge were also significantly associated with the patterns obtained. This was an important paper in that it was one of the first, using new multivariate analytical methods, to highlight the effects of acidity on stream communities, though there had been previous work on acidity. Such information has been of use in establishing the impact of acidification on freshwater communities in the UK (UKAWRG 1988) and elsewhere. This and other similar surveys (Wright *et al* 1984; Ormerod & Edwards 1987; Rutt *et al* 1990; Boulton & Lake 1992), focus on the spatial variation in communities (at the between-stream scale) in relation to environmental heterogeneity. From this descriptive research there led two main lines of enquiry. First, small scale analytical and experimental studies sought "process-level" explanations for the spatial patterns revealed. In the Ashdown Forest study, for instance, there were investigations of shredding invertebrates (Groom & Hildrew 1989; Dobson & Hildrew 1992) and herbivory (Winterbourn *et al* 1985; Winterbourn *et al* 1992). The second line of enquiry had mainly an applied or strategic focus and asked whether the spatial patterns in benthic community structure were temporally stable. If so, any changes in benthic communities that do occur through time can be used to detect environmental change, whether in acidity or climate. This is the purpose of biomonitoring (Rosenberg & Resh 1993) and is the rationale behind various surveillance initiatives; for instance the United Kingdom's Acid Waters stream Monitoring Network (see Chapter 5).

The two approaches outlined above - "process studies" and biomonitoring - are related. This is because ecological interactions, underlying community structure and spatial patterns, may determine natural temporal variation in communities (even in the absence of environmental change) in addition to community responses to a directional environmental "signal" (for instance caused by reduced acidic depositions). Distinguishing such "noise" from a genuine community response to environmental change is a major challenge to biomonitoring.

Townsend *et al* (1987) tried to bridge the gap between the two approaches by resampling the benthic communities of the Ashdown Forest in 1984, and relating community persistence to known environmental variables. Their purpose was to study temporal variation in well-studied streams in which something was known of underlying ecological interactions. Twenty-seven of the original thirty-four sites were resampled using the same methods of collection. They used a variety of techniques to examine community change, and they then compared the collections from the two occasions in terms of species composition and of relative abundance. Persistence in species composition was measured using Jaccard's index of similarity, and by the number of the 15 most abundant species in the 1976 survey still present in 1984. Persistence in relative abundance was assessed by correlating the rank abundance of species in 1976 with that of 1984 using Spearman's r. Spearman's correlation coefficients are a frequently used approach to the measurement of similarity described in every statistics text book (e.g., Sokal and Rohlf 1981, Chapter 15). With regards to temporal patterns, persistence of invertebrate communities was found to be higher at sites close to the source, and which were of low pH and low summer temperature. These streams tended to be those with the most retentive channels. For spatial patterns, ordination of the communities established that pH and distance from the source of the streams to be highly correlated with Axis 1 and 2 respectively. Other research confirms the relationship between acidity and benthic invertebrates (Bell 1971; Sutcliffe & Carrick 1973; Sutcliffe & Hildrew 1989; Smith *et al* 1990).

Measuring the persistence of communities requires monitoring on at least two occasions. These should be separated by sufficient time to allow at least one complete turnover of the population, to avoid resampling the same individuals (Connell & Sousa 1983). Relatively few studies, however, have looked rigorously at lotic communities over long periods of time. There are essentially two approaches which can be taken for any given level of effort. First, one can look at a large number of sites, but on only two or a few occasions several years apart (Weatherly & Ormerod 1990). Secondly, one can look at one or a few streams regularly over a number of years (McElravy *et al* 1989; Giller *et al* 1991). These two approaches both have their drawbacks. The first has too few replicates in time and the second too few replicates in space.

In the study of Townsend *et al* (1987) there were a "large" number of streams (n = 27), within a small geographical area, sampled twice over a period of eight years, an example of the first of the two approaches outlined above. In my study I took the opportunity to repeat the survey of Townsend *et al's* (1983, 1987) sites, thus increasing the time scale to thirteen years. Because of disturbance to some streams or access problems the number of sites available for comparison across all three years was twenty-six, still a substantial number. My objectives were:

i) to see if the spatial patterns among sites revealed in the two earlier surveys were robust.

ii) to see if the pattern of persistence among sites revealed by Townsend *et al* (1987) were repeatable.

4.ii METHODS.

Invertebrate sampling.

The sites in this survey lie in the headwaters of the River Medway and the Sussex Ouse, (Fig. 2.2). The Medway flows north to join the river Thames, while the Ouse flows south to the English Channel at Newhaven. Twenty-six stream riffle sites were sampled in October 1989, at the same time of year as the two previous surveys. Broadstone stream, the most intensely studied stream in the Ashdown Forest, was for some reason left out of the original suite of sites, and was not included in the second survey. Data from Broadstone stream has been included in the 1989 study and I have used data from past studies on Broadstone stream where feasible. Five Surber sample-units (area 0.0625 m^2, 330 μm mesh size) were taken at random from riffles sites. The substrate was removed to a depth of approximately 5cm and all the material collected was preserved in the field using 70% Industrial Methylated Spirits (IMS). Gravel and debris were removed by elutriation in the laboratory and the animals were hand sorted, identified to species where possible and counted. Some groups, particularly those whose populations are dominated in autumn by very small individuals, gave particular taxonomic difficulties. This was true of the "long-legged" Nemouridae - (*Nemoura avicularis* and *N. cinerea)* and of the Chironomidae. A conservative approach was taken in such cases, so as not to risk spurious or apparent community changes between sampling years. Chironomidae were identified to tribe and the genus *Nemoura* to long-legged or short-legged (mainly *N.cambrica & N.erratica*) forms.

Environmental variables

Minimum and maximum water temperature (^oC), pH and conductivity (μScm^{-1}, 25^oC) were recorded when each sample was taken in autumn 1989, using the PTI - 20 digital pH and conductivity meter. Other variables obtained on previous sampling occasions were included - such as range in discharge ($m^3\ s^{-1}$), impoundment linkage (the number of lakes above the site location) and stream link magnitude (the number of tributaries upstream of the site). Details of collection of environmental variables are given in greater detail in Chapter 2.

Statistical analysis

A matrix of species by site was constructed and the raw data from 1976 and 1984 were added to the 1989 data. Sample units were pooled. As the counts had a negative binomial distribution they were transformed by $\log_{10}(x+1)$ (Elliott 1977), and the adequacy of the transformation was confirmed by plotting the means before and after the transformation. Bartlett's test was used to test for homogeneity of variances or *homoscedasticity*. The null hypothesis tested is that all the variance estimates being compared are estimates of the same variance.

For measures of persistence in species composition, Jaccard's and Sorenson's indices were used. There are more than two dozen similarity measures available (Wolda 1981), and some confusion has arisen over the best method to use. The simplest measures of similarity are the binary similarity coefficients which deal with presence/absence data,

where a = the number of species in sample A and sample B

b = the number of species in sample B but not in sample A

c = the number of species in sample A but not in sample B

d = the number of species absent in both samples.

There is some question as to whether or not d is a biologically significant number. It may be meaningful where there is an absence from a well known community of a particular species but, conversely, elephants are always absent from plankton samples! For this reason d is usually omitted from similarity measures.

The equations for both Jaccard's and Sorenson's index are given in Chapter 3.

Sorenson's and Jaccard's similarity coefficients have both been used. Jaccard's was the similarity coefficient used in comparing 1976 and 1984 data (Townsend *et al* 1987). Sorenson's coefficient weights matches in species composition more heavily than mismatches, so that if many species are present within a community, but not present in a particular sample from that community, it is therefore useful in some cases to use Sorenson's coefficient rather than Jaccard's. Sorenson's and Jaccard's coefficients are calculated for 1976-1984, 1984-1989 and 1976-1989.

Relative abundances were used to assess persistence in species ranking. This gives another approach to measuring similarity using correlation coefficients. Here, the strength of the association between two sets of measurements are considered. To avoid the assumption of linearity, Spearman's r is used instead of Pearson's product-moment correlation coefficient r, as a measure of similarity. Correlation coefficients are most useful in low-diversity communities with a reasonable sample size (Krebs 1989). In this survey, the correlation coefficient between the rank abundances in 1976, 1984 and 1989 were calculated for the complete community, and for Plecoptera and Chironomidae separately, as measures of persistence between years. Value of r_S range from -1 to +1, where +1 indicates a perfect positive correlation and -1 a perfect negative correlation.

The data set, a species/sample matrix, was put into a suitable format using the FORTRAN program COMPOSE from the Cornell Ecology Program (C.E.P). Ordination was carried out to detect groups of similar samples and to display their similarities in low dimensional space (Gauch 1982), using DEtrended CORrespondence ANAlysis (DECORANA). This is an improved ordination technique replacing reciprocal averaging (RA). Reciprocal averaging has two inherent problems. Firstly, the 'arch' or 'horseshoe' effect compresses the axes (Gauch *et al* 1977; Kendall 1975). The arch effect arises from a mathematical artifact and for the two axes to be interpreted separately they need to be independent, not just uncorrelated. The second problem is the distortion of relative distances between samples and species. DECORANA uses detrending in place of orthogonalization. This is followed by standardization of unit within-sample variance to overcome these problems, and serves to summarize community data by producing a low-dimensional ordination space, in which similar species and samples are grouped close together and dissimilar entities far apart. Because the calculations do not depend on the square or cube of the number of samples or species, there is no difficulty in analysing large data sets, giving DECORANA an advantage over other ordination programs such as Hybrid non-metric MultiDimensional Scaling (HMDS) (Faith *et al* 1987). A score for each axis is calculated for each site and can be used to correlate the ordination with environmental variables.

No down weighting of rare species was employed. This is a method used to avoid distortion, although rare species are often found at the edges of the ordination diagram, and occur there because they are associated with extreme environmental conditions (ter Braak & Prentice 1988). They are, in this situation, often the very species indicative of acid conditions. The relative strengths of the axes are given in eigenvalues, and the importance of each axis in explaining the variance in the data set is found by dividing the sum of all the eigenvalues by the value that is given for that axis. Pearson's product-moment correlation coefficients between site scores on DECORANA axes 1, 2 and 3 and environmental variables for the three years were computed to help interpret the ordination patterns. Where required, variables were transformed to normalise their distribution using Ln. or Log_{10}.

Two-way indicator species analysis (TWINSPAN) (Hill *et al* 1975; Hill 1979a), is another FORTRAN program - a classification technique used to complement the ordination results. This is a polythetic divisive technique using reciprocal averaging separately to ordinate the data subsets which are produced in the program, and it illustrates the hierarchical relationship between communities. TWINSPAN uses information on all the species and uses separate ordinations for each subset it produces. The communities are progressively divided into smaller subsets according to the degree of similarity of species composition. At each division, 'indicator' species are shown. Caution should be exercised over the use of the word 'indicator' (Hill 1979b), however. Using the program COMPOSE to set the data in the correct format, data were then transformed into semiquantitative 'pseudospecies', with each pseudospecies representing an abundance range of the original species. Four cut-off levels were chosen,

Pseudospecies	Abundance range
1	1-10
2	11-100
3	101-1000
4	1000 +

A species with an abundance of 1000+ is treated as four pseudospecies and, at each level, the pseudospecies are treated separately. After three divisions the TWINSPAN procedure was terminated as further divisions would have been ecologically meaningless.

Canonical analysis is essentially an extension of DECORANA, in that it allows species, sites and environmental variables to be plotted together in low dimensional space, thereby giving information about species-environment relations from data on biological communities and their environment. It can be used as an alternative method of detrending. The program used is written in FORTRAN and is called CANOCO (ter Braak 1987), CANOnical Community Ordination and uses a general iterative ordination algorithm. The data sets are exactly the same as for the C.E.P. programs (a species by site matrix), with the addition of an extra data matrix (the environmental variables), which are incorporated into the program separately. Initially the data matrix is required in the SYLK condense format and is then 'condensed' before the analysis. SYLK is a file format and the Cornell condensed format turns the data matrix into machine readable copy for the Cornell Ecology Programs. The type of analysis carried out here was CCA, Canonical Correspondence Analysis, and the results are produced in the form of a biplot.

4.iii RESULTS.

4.iv. Physicochemical variables.

A total of 26 stream sites were compared between years (1976, 1984 & 1989). Mean pH values are compared in Fig 4.1: not surprisingly, correlations of pH at the sites between the years (a) 1976/84, (b) 1984/89 and (c) 1976/1989, are all significant ($p < 0.001$) For (a) and (b) the regression coefficients between years do not significantly differ from the null hypothesis that

$pH_{\text{year } x} = pH_{\text{year } x+1}$.

A matrix of Pearson correlation coefficients between physicochemical variables is presented in Table 4.1 and physicochemical variables for each site are presented in Table 4.2: for the year 1989.

Table 4.1: Matrix of Pearson correlation coefficients between physicochemical variables measured at twenty-six stream sites.
Correlation's significantly different from zero, *p <0.05, $r = 0.315$; **p<0.01, $r = 0.437$; ***p<0.001, $r = 0.559$.

	mean pH	min pH	max pH	mean T	July T	Cond	Disch	Imp	link
Dist	0.8***	0.39*	0.08	0.03	0.19	0.15	0.86***	0.78***	0.85***
	mean pH	0.91***	0.74***	0.56***	0.58***	0.26	0.21	0.28	0.35*
		min pH	0.64**	0.55**	0.60***	0.22	0.40*	0.40*	0.46**
			maxpH	0.54**	0.48**	0.52**	0.20	0.26	0.35*
				mean T	0.97***	0.33*	0.28	0.10	0.35*
					July T	0.23	0.22	0.02	0.34*
						Cond	0.38*	0.52**	0.43*
							Disch	0.79***	0.78***
								Imp	0.75***
									Link

Site No.	Distance from Source (Km).	Mean pH.	pH Range.	Temperature Mean (°C).	Temperature July (°C).	Conductivity (μScm^{-1}).	Mean annual Discharge. (m^3s^{-1}).	Impoundment Linkage.	Stream Link Magnitude.
LP	0.61	6.4	5.6-7.0	8.4	13.9	125	0.04	0	1
WR	1.75	6.7	6.5-6.8	8.3	17.1	202	0.06	0	1
KBP1	1.77	5.9	5.6-6.4	8.6	15.3	153	0.06	0	1
KBP2	1.82	5.5	5.2-5.8	8.6	14.4	222	0.06	0	1
NBG	3.90	6.2	5.4-6.7	8.7	15.0	211	0.08	0	2
OL1	1.72	4.6	4.2-4.9	8.4	15.5	98	0.05	0	1
OL2	2.40	4.7	4.4-5.2	8.3	15.7	102	0.06	0	1
CH	2.10	5.0	4.7-6.2	8.6	14.6	112	0.08	0	1
LO	1.82	4.8	4.4-5.3	8.5	15.0	105	0.06	0	1
CW	1.27	6.7	6.3-7.2	8.6	16.0	216	0.04	0	1
NU*	0.56	6.8	6.5-7.3	8.9	16.3	229	0.03	0	2
CS*	1.21	6.6	6.2-6.8	8.8	14.7	230	0.13	0	2
DB*	1.64	6.4	6.0-6.7	9.2	16.1	130	0.08	0	3
OLS*	1.80	6.8	6.3-6.9	9.5	16.7	158	0.11	1	2
FW*	2.58	5.9	5.4-6.7	8.7	16.0	188	0.20	1	3
MH1	4.73	6.8	6.4-7.2	8.6	15.9	176	0.24	2	6
MH2	4.83	6.4	6.0-6.7	8.6	16.0	181	0.26	2	6
BFG	5.41	6.5	6.3-6.8	8.5	16.1	187	0.20	2	6
OF*	3.19	6.7	6.2-7.2	9.6	16.7	197	0.18	1	6
BBG*	6.05	7.0	6.7-7.2	9.7	17.0	225	0.40	2	8
HL*	3.14	6.7	6.5-6.9	9.1	16.4	171	0.25	1	3
MF*	5.29	6.5	6.3-7.0	9.5	16.6	198	0.30	2	3
MG	9.54	6.6	6.4-6.8	9.6	16.8	134	0.43	2	9
PB	11.08	6.6	6.4-6.9	9.4	16.7	168	0.36	2	10
HMI	6.30	6.5	6.3-7.0	9.5	16.6	235	0.39	2	9
WY	9.29	6.8	6.6-7.2	9.7	16.8	227	0.44	3	11
WH	8.22	6.9	6.5-7.1	9.7	16.7	273	0.41	3	10
BWM*	2.35	6.8	6.5-7.1	10.1	17.3	199	0.13	1	6
BS	0.42	5.3	4.8-6.0	8.5	15.4	86	0.06	0	1

Table 4.2: VALUES OF PHYSICOCHEMICAL VARIABLES FROM 29 STREAM SITES OF THE ASHDOWN FOREST. Sites marked * are tributaries of the River Ouse; the remainder are part of the River Medway system. (1989).

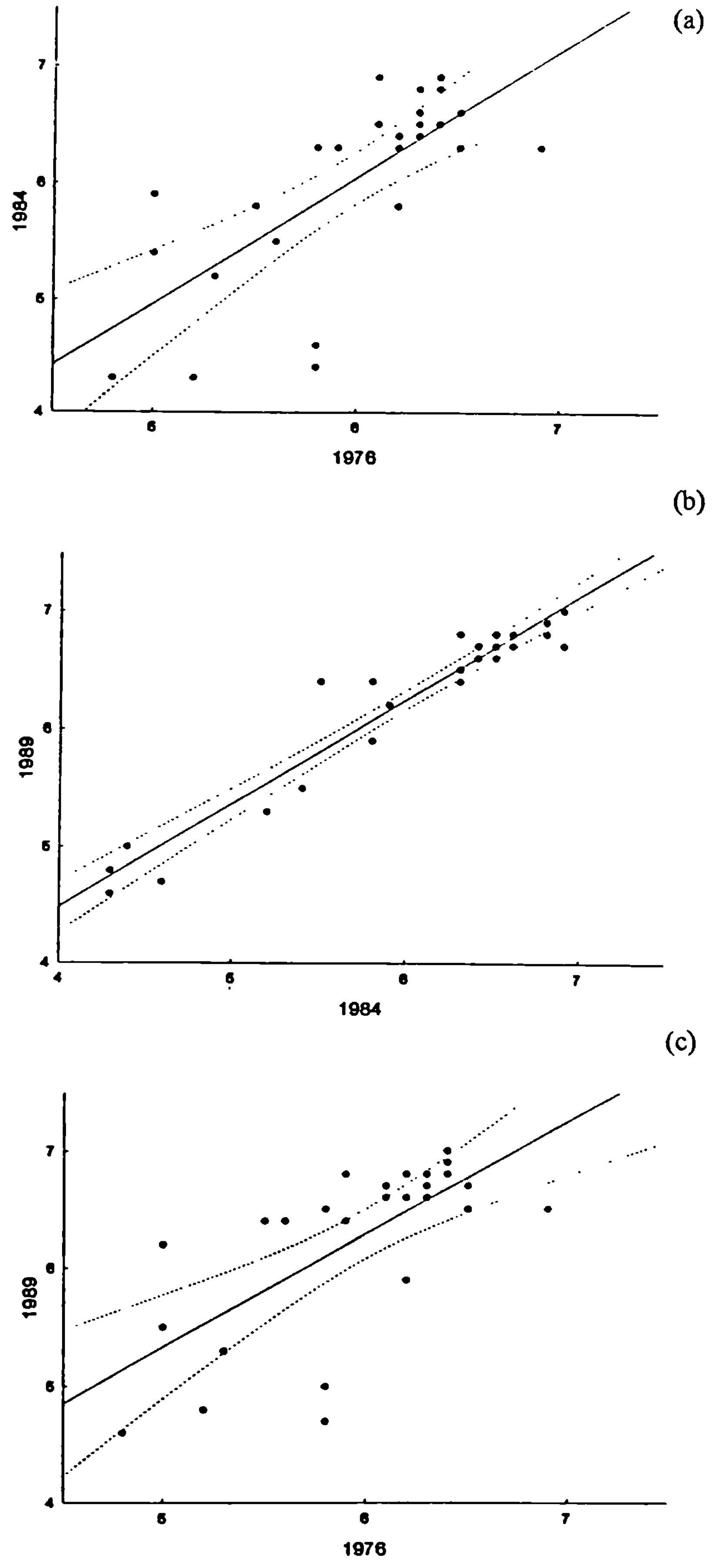


Fig. 4.1: Plot of mean annual pH (a) in 1976 against that in 1984, (b) pH in 1984 against that in 1989 and (c) pH in 1976 against that in 1989, for 26 stream sites. Product moment correlation coefficients, r = 0.75, r = 0.96 and r = 0.48 for a, b and c respectively. The line was derived from regression, and the 95% confidence limits are given.

Sites with low pH values are those close to source, have low discharge and low summer temperatures (Fig 4.2 a, b & c, respectively). Distance from source, mean annual discharge and July temperatures are all significantly correlated with mean pH.

4.v. Persistence

Measures of persistence plotted against pH and summer temperature, for the years 1976-84, 1984-89 and 1976-89, are shown in Fig 4.3. In this example, Sorenson's index is used as the persistence measure. Stream sites with low pH and low summer temperatures have a high persistence and the same general pattern is revealed when persistence is plotted against either variable (Fig 4.3)

Spearman's rank correlation coefficients for the relative abundance of the total community and Plecoptera are plotted against pH and July temperatures in Fig 4.4. Again we see that correlation coefficients for the whole community are greater than +0.5 and are therefore significant for sites with low pH and low summer temperatures. Points which occur over to the right hand side of the graphs occasionally score high, but these sites do not have a significant Spearman's $_r$ between years. Table 4.3 lists the measures of persistence and rank abundances for 29 stream sites. Due to a variety of difficulties, a few sites were not sampled on more than one occasion, and these data are missing from the Table. For the Spearman's rank correlation coefficients on Plecoptera, some sites were omitted. These were stream sites where less than seven pairs of variables were available for the calculations. Pearson product moment correlation coefficients between community persistence measures and environmental variables (Table 4.4) were significant mainly for minimum pH and summer temperatures.

4.vi Spatial relationships.

The ordination results for the years 1976, 1984 and 1989 are plotted in Fig 4.5. Axis 1 is highly significantly correlated with mean annual pH. Acid sites are circled in red

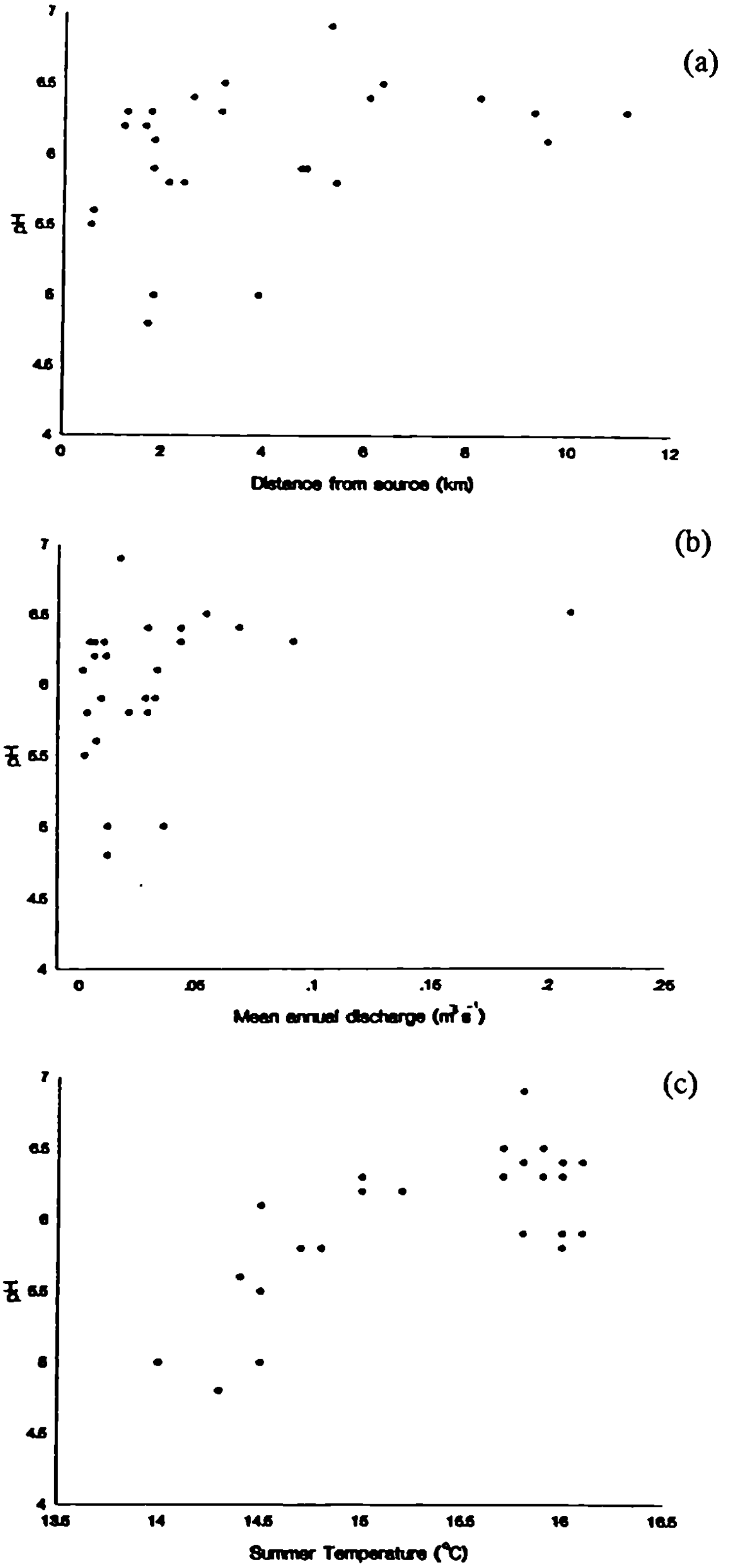


Fig. 4.2: Plot of environmental variables, distance from source (a), mean annual discharge (b) and summer temperature (c) plotted against pH. Stream sites with low pH are located close to source, have a low discharge and low summer temperatures.

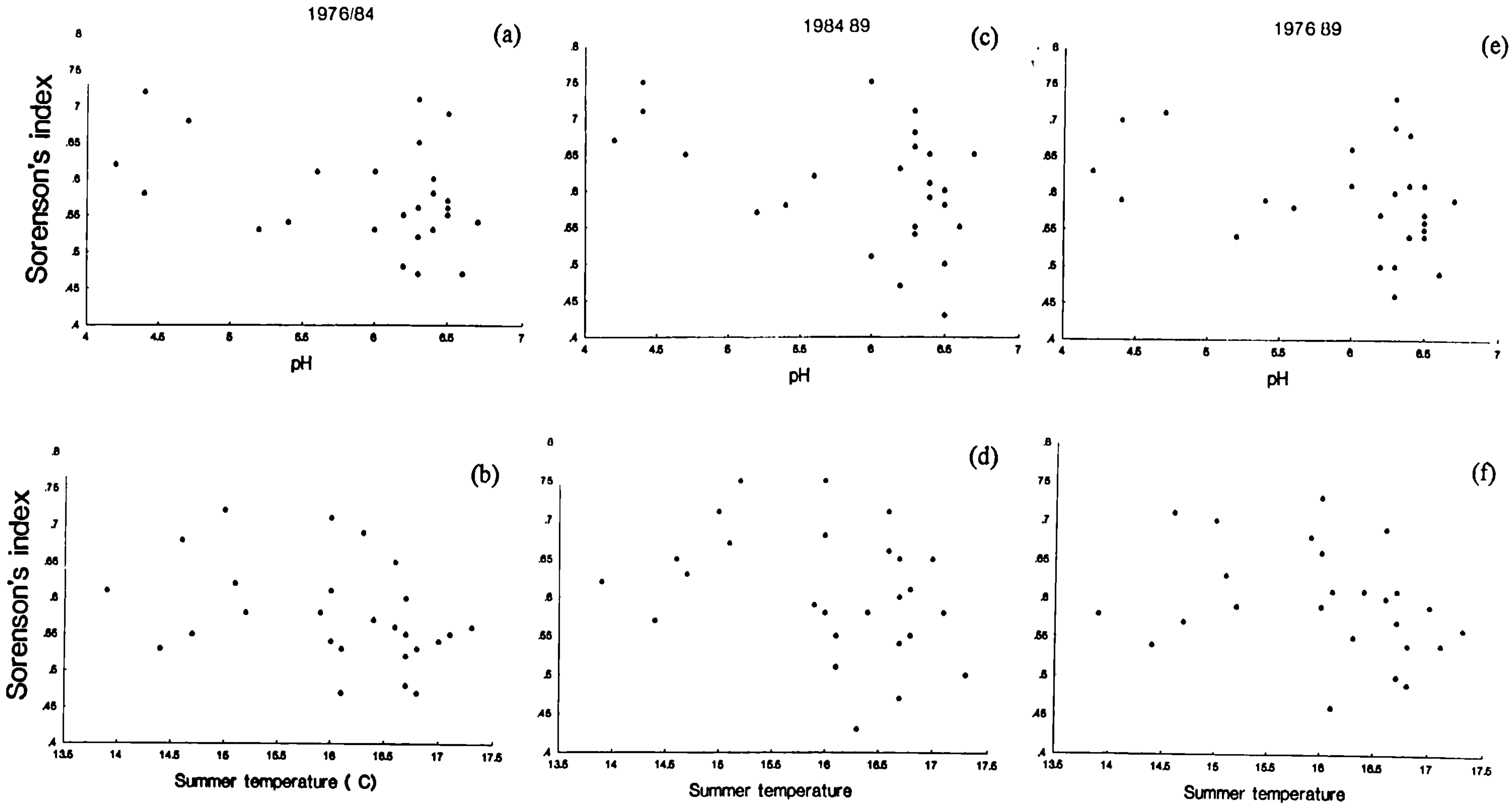


Fig. 4.3: A persistence measure (Sorenson's index) for the years 1976/1984, 1984/89 and 1976/89 (a,c & e), plotted against mean annual pH, and against summer temperature (b,d & f). Streams with low pH and low summer temperature generally have a high persistence measure.

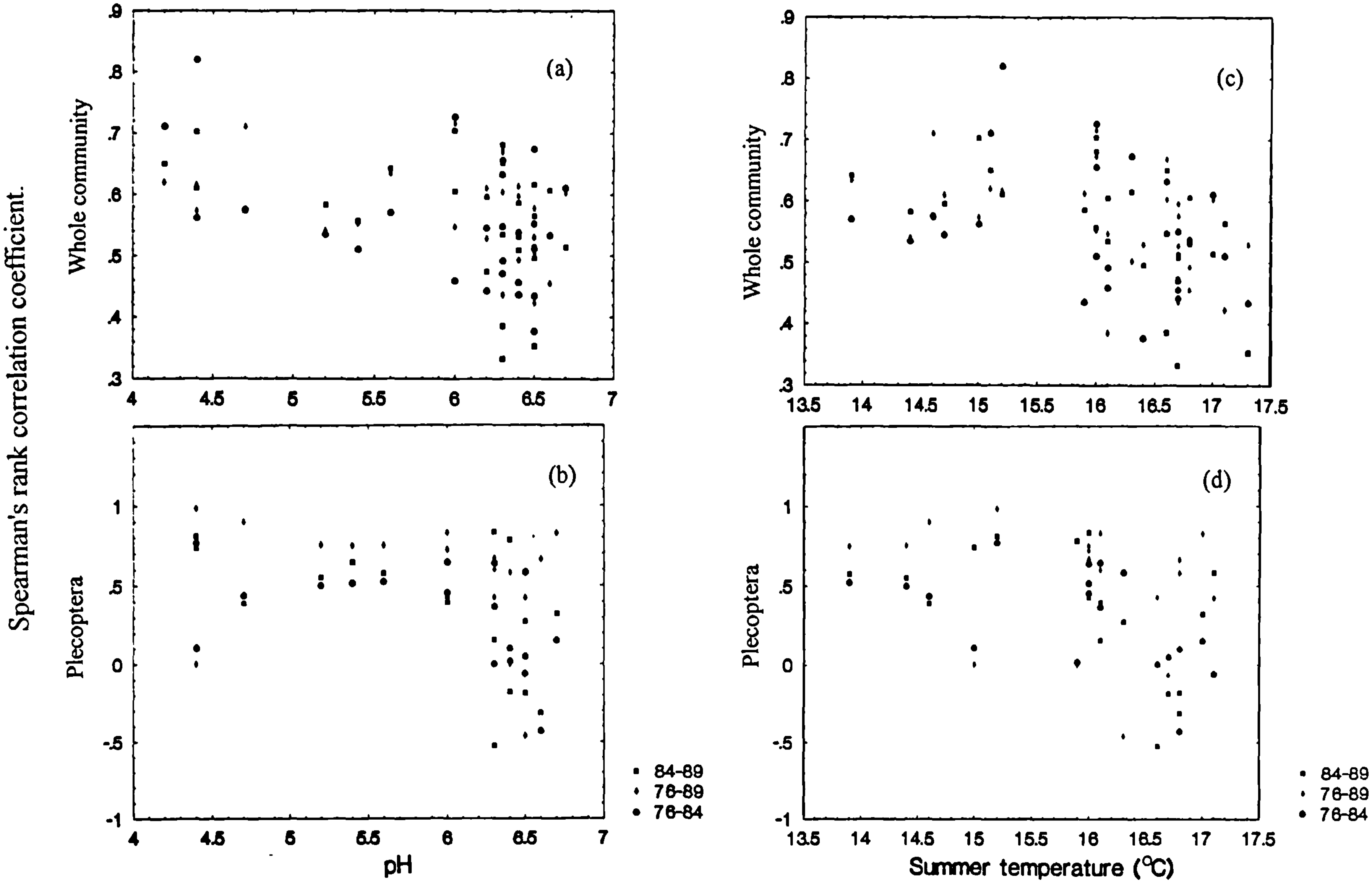


Fig 4.4: Plots of rank abundances (Spearman's) against environmental variables. (a) r_s for the total community against pH and (b) r_s for Plecoptera against pH. (c) r_s for the total community against temperature and (d) r_s for Plecoptera against summer temperature. Spearman's r has been calculated for the years 1976-84, 1984-89 and 1976-89.

SITE	JACC1	JACC2	JACC3	SOR1	SOR2	SOR3	SPR1	SPR2	SPR3	PLEC1	PLEC2	PLEC3	CHI1	CHI2	CHI3
LP	0.43	0.42	0.45	0.55	0.58	0.62	0.570	0.634	0.642	0.525	0.750	0.575	0.241	0.441	0.021
WR	0.47	0.36	0.41	0.46	0.54	0.58	0.511	0.423	0.564	-0.061	0.422	0.581	0.216	0.035	0.001
KBP1	-	0.36	-	-	0.53	-		0.441	-	-	-	-	-	-	-
KBP2	0.41	0.37	0.40	0.50	0.54	0.57	0.535	0.541	0.583	0.500	0.754	0.754	0.204	0.181	-0.511
NBG	-	0.30	-	-	0.41	-	-	0.303	-	-	-	-	-	-	-
OL1	0.48	0.45	0.50	0.61	0.63	0.67	0.711	0.620	0.650	-	-	-	0.411	-0.212	0.154
OL2	0.41	0.42	0.60	0.53	0.59	0.75	0.82	0.617	0.611	0.771	0.985	0.812	0.054	0.297	0.031
CW	0.47	0.55	0.49	0.62	0.71	0.65	0.576	0.711	0.574	0.438	0.899	0.391	0.268	-0.022	-0.003
LO	0.55	0.54	0.55	0.69	0.90	0.71	0.563	0.574	0.703	0.107	0.001	0.741	0.281	0.311	0.610
CW	0.55	0.60	0.51	0.64	0.73	0.68	0.656	0.673	0.681	0.638	0.669	0.834	-0.072	0.064	0.463
NU	0.50	0.41	0.50	0.47	0.55	0.43	0.674	0.503	0.616	0.581	-0.462	0.273	0.042	-0.325	0.561
CS	0.48	0.40	0.46	0.53	0.57	0.63	0.545	0.610	0.596	-	-	-	-0.129	0.054	-0.426
DB	0.46	0.44	0.34	0.61	0.61	0.51	0.459	0.547	0.605	0.643	0.828	0.396	-0.169	0.003	-0.305
OLS	0.30	0.33	0.37	0.49	0.50	0.54	0.471	0.436	0.333	-	-	-	-0.036	0.377	0.187
FW	0.40	0.40	0.41	0.60	0.59	0.58	0.511	0.553	0.557	0.516	0.750	0.645	0.048	-0.081	0.571
MH1	0.58	0.51	0.42	0.51	0.68	0.59	0.436	0.613	0.586	0.018	0.001	0.783	-0.114	0.428	-0.399
MH2	0.56	0.49	0.69	0.65	0.66	0.75	0.726	0.716	0.704	0.454	0.722	0.431	0.424	0.742	0.430
BFG	0.39	0.31	0.40	0.42	0.46	0,55	0.492	0.385	0.535	0.368	0.600	0.156	0.563	0.027	-0.015
OF	0.33	0.33	0.31	0.51	0.50	0.47	0.442	0.528	0.474	-	-	-	0.138	0.498	0.031
BBG	0.42	0.42	0.48	0.58	0.59	0.65	0.611	0.603	0.514	0.512	0.825	0.323	0.015	0.392	-0.028
HL	0.39	0.44	0.32	0.48	0.61	0.58	0.377	0.530	0.496	-	-	-	-0.367	0.785	0.031
MF	0.50	0.53	0.55	0.63	0.69	0.71	0.633	0.699	0.651	-	-	-	0.238	0.039	0.104
MG	0.42	0.37	0.44	0.57	0.54	0.61	0.538	0.493	0.531	0.101	0.580	-0.179	-0.270	-0.067	0.623
PB	0.44	0.44	0.36	0.47	0.61	0.65	0.456	0.597	0.509	-	-	-	-0.322	0.421	-0.371
HMI	0.48	0.43	0.50	0.63	0.60	0.66	0.548	0.604	0.386	0.001	0.426	-0.525	-0.117	0.502	0.001
WY	0.56	0.32	0.38	0.48	0.49	0.55	0.533	0.455	0.607	-0.429	0.664	-0.311	-0.277	0.503	-0.131
WH	0.47	0.40	0.43	0.60	0.57	0.60	0.552	0.577	0.514	0.048	-0.068	-0.187	-0.196	0.061	0.265
BWM	0.29	0.39	0.33	0.54	0.56	0.50	0.434	0.529	0.353	-	-	-	-0.313	0.202	0.132
BS	-	-	0.35	-	-	0.52	0.458	0.259	0.272	-	-	-	-	-	-

Table 4.3: Measures of community persistence. Derived from twenty-nine stream invertebrate communities.
Key: JACC, Jaccard's index of similarity in community composition; SOR, Sorenson's index of similarity; SPR, Spearman's rank correlation coefficient calculated for the whole community; PLEC and CHI are Spearman's correlation coefficients for Plecoptera and Chironomidae, respectively. Numbers 1-3 are the years, 1 = 1976-1984, 2 = 1976-1989 and 3 = 1984-1989.

Table 4.4 : Pearson product moment correlation coefficients between measures of community persistence and physicochemical variables in the twenty-six sites. (Coefficients significantly different from zero: *$p < 0.05$, **$p < 0.01$).

Measure of persistence	Mean pH	Min pH	Max pH	Mean temp	July temp	Conductivity
JACC 1	0.19	0.16	0.24	-0.03	0.04	0.07
JACC 2	-0.29	-0.35*	-0.15	-0.31	-0.42*	-0.33
JACC 3	-0.34	-0.35*	-0.33	-0.30	-0.23	-0.24
SOR 1	-0.37	-0.33	-0.41	-0.26	-0.34	-0.20
SOR 2	-0.32	-0.39*	-0.19	-0.30	-0.42*	-0.36*
SOR 3	-0.46*	-0.46*	-0.48*	-0.22	-0.27	-0.36*
SPR 1	-0.31	-0.31	-0.32	-0.21	-0.18	-0.13
SPR 2	-0.30	-0.36*	-0.16	-0.11	-0.41*	-0.20
SPR 3	-0.30	-0.35*	-0.32	-0.51**	-0.40*	-0.38*
PLEC 1	-0.40*	-0.45*	-0.35*	-0.50	-0.52**	-0.34
PLEC 2	-0.30	-0.28	-0.28	-0.07	-0.20	-0.33
PLEC 3	-0.44*	-0.49*	-0.44*	-0.80**	-0.52**	-0.43*
CHI 1	-0.39*	-0.38*	-0.40*	-0.70**	-0.44*	-0.23
CHI 2	-0.00	-0.00	-0.08	0.10	0.02	0.05
CHI 3	-0.02	-0.05	0.03	0.01	0.18	-0.09

and include Lavender Platt, Kidbrook Park, Old Lodge 1 & 2, Chuck Hatch and Lone Oak. Axis 2 is correlated with summer temperatures. Axes 1 and 2 accounted for 73.7% of the variation in 1989, 81.6% in 1984 and 72.5% in 1976, and Axis 1 accounted for over 50% of the variation in 1976 and 1984 (Table 4.5). Broadstone Stream, site 35, is included in the results and falls within the red circle, as a site significantly related to pH. Nutley (NU), is situated centre-top of the ordination for all years; and although this site is circum-neutral it has, on occasion, a species composition similar to the acid sites.

Table 4.6 gives the results of the product moment correlation between physico-chemical variables and scores for the DECORANA axes 1, 2 and 3. The most significant correlation's are for pH (r = -0.71 for 1989), and for temperature (r = -519 and r = -0.646 for the years 1976 and 1984, respectively). On axis 2 July temperature is significant in 1989, there are no significant variables for1984, and the most significant variable in 1976 is distance from source. All the variables, apart from stream link magnitude, discharge and distance from source, are significantly correlated with the first two DECORANA axes in 1989 and all are significant for the first axis in 1976. The variables which showed correlation with axis 3 were mean annual discharge, distance from source and impoundment linkage.

The TWINSPAN site classification depicts a dendogram to two levels (Fig 4.6). The suffix *a* refers to the community composition in 1976, *b* to 1984 and *c* to 1989. At the first level sites separate out to acid and circumneutral streams and for most sites this is consistent for all three sampling occasions. The indicator species listed for the first negative are acid tolerant species, *Leuctra nigra* and *Plectrocnemia conspersa.* The first positive division lists *Baetis spp* and *Gammarus pulex*, both intolerant of low pH.

The second negative division separated out on summer temperature with the sites with the negative divisions having lower summer temperatures. The nemourid stoneflies were found at varying pseudospecies levels at most sites. Although the majority of sites separated out together for the three sampling occasions, Fairwarp c separated into the first negative division, as did sites Marden's Hill 2 bc and Boringwheel Mill bc.

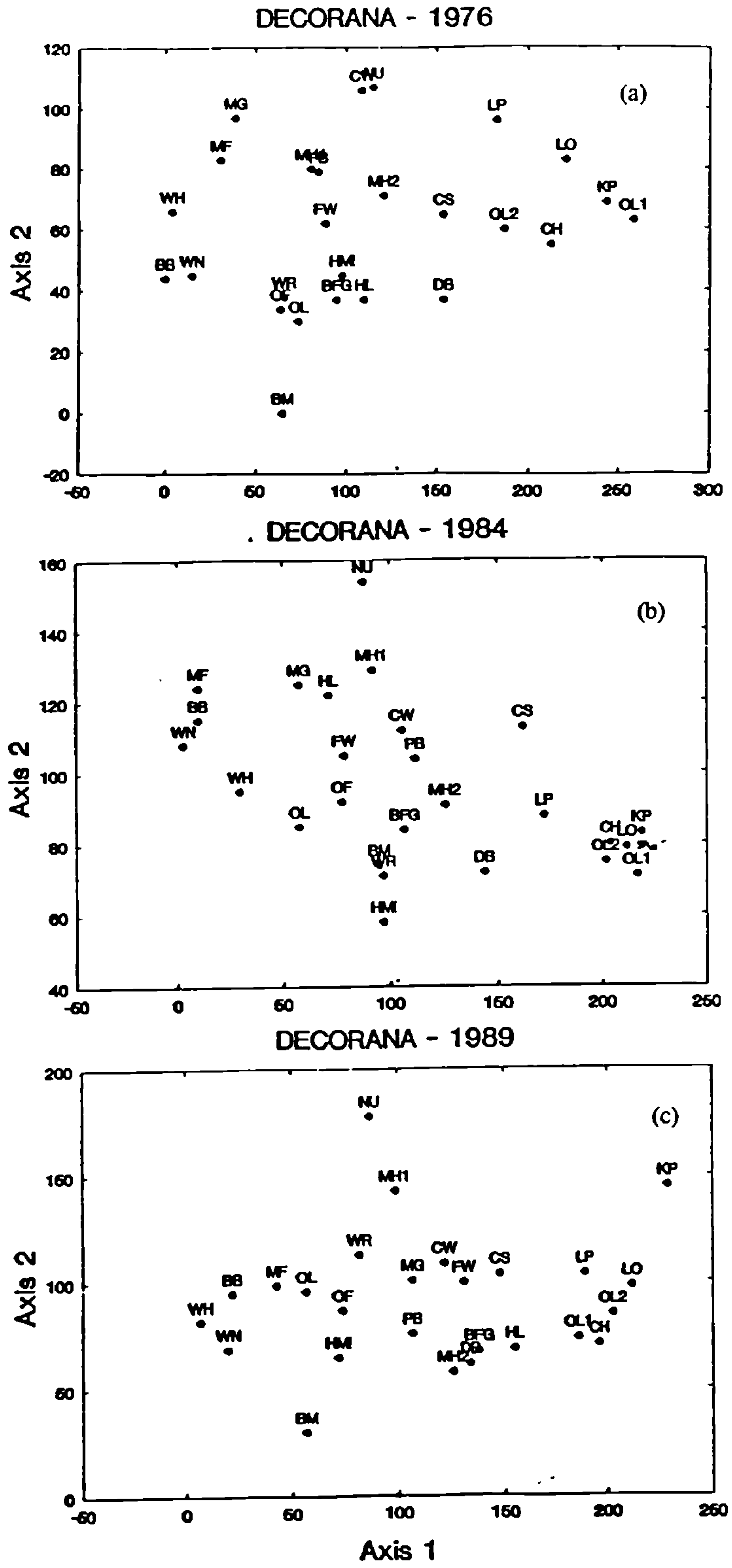


Fig. 4.5: Ordination of sites using DECORANA for the years 1976 (a), 1984 (b) and 1989 (c). The first axis is strongly correlated with pH and the second axis with summer temperature. The acid sites are circled. In ordination space these sites can be seen to have values in the region of 200 on axis 1 and approximately 100 on axis 2. Site abbreviations are given in Chapter 2.

Table 4.5: Eigenvalues, percentage and cumulative percentage variance explained and lengths (in standard deviations) of DECORANA axes for 1989, 1984 & 1976.

A: 1989

	Eigenvalue	% var explained	cum % explained	length (S.D)
AXIS 1	0.474	44.3	44.3	2.21
AXIS 2	0.323	29.4	73.7	1.90
AXIS 3	0.151	18.6	92.3	1.36
AXIS 4	0.091	7.7	100.0	1.84

B: 1984.

	Eigenvalue	% var explained	cum % explained	length (S.D)
AXIS 1	0.525	51.6	51.6	2.42
AXIS 2	0.310	30.0	81.6	1.73
AXIS 3	0.264	13.8	95.4	1.57
AXIS 4	0.014	4.6	100.0	2.40

C: 1976.

	Eigenvalue	% var explained	cum % explained	length (S.D)
AXIS 1	0.562	59.2	59.2	1.97
AXIS 2	0.323	23.1	72.5	1.54
AXIS 3	0.111	18.5	91.0	2.11
AXIS 4	0.099	9.0	100.0	1.44

Table 4.6 : Product-moment correlation coefficient between site scores on DECORANA axes 1, 2 and 3 and environmental variables.

A: 1989.

	AXIS 1	AXIS 2	AXIS 3
Distance from source	-0.217	0.031	-0.459*
Mean pH	-0.595**	-0.003	0.111
Minimum pH	-0.490*	-0.127	0.131
Maximum pH	-0.734***	0.145	0.112
Mean temperature	-0.711***	-0.310	0.392*
July temperature	-0.646***	-0.403*	0.456*
Conductivity	-0.668***	-0.233	-0.193
Mean annual discharge	-0.361	0.082	-0.526*
Impoundment linkage	-0.463*	0.068	0.542**
Stream link magnitude	-0.384	-0.176	-0.318

B: 1984.

	AXIS 1	AXIS 2	AXIS 3
Distance from source	-0.199	0.223	-0.430*
Mean pH	-0.402*	0.085	-0.166
Minimum pH	-0.395*	0.127	-0.187
Max pH	-0.488*	0.080	-0.094
Mean temperature	-0.519*	-0.164	-0.019
July temperature	-0.439*	-0.189	0.082
Conductivity	-0.399*	-0.336	0.229
Mean annual discharge	-0.452*	0.272	-0.504*
Impoundment linkage	-0.384*	0.139	-0.394*
Stream link magnitude	-0.121	-0.100	-0.294

C: 1976.

	AXIS 1	AXIS 2	AXIS 3
Distance from source	-0.397*	0.570**	-0.279
Mean pH	-0.533*	-0.270	-0.039
Minimum pH	-0.495*	-0.177	0.074
Maximum pH	-0.595**	-0.274	0.017
Mean temperature	-0.646***	-0.310	0.236
July temperature	-0.594**	-0.396*	0.323
Conductivity	-0.481*	-0.228	-0.056
Mean annual discharge	-0.530*	0.523*	-0.311
Impoundment linkage	-0.518*	0.453*	-0.547**
Stream link magnitude	-0.424*	0.212	-0.245

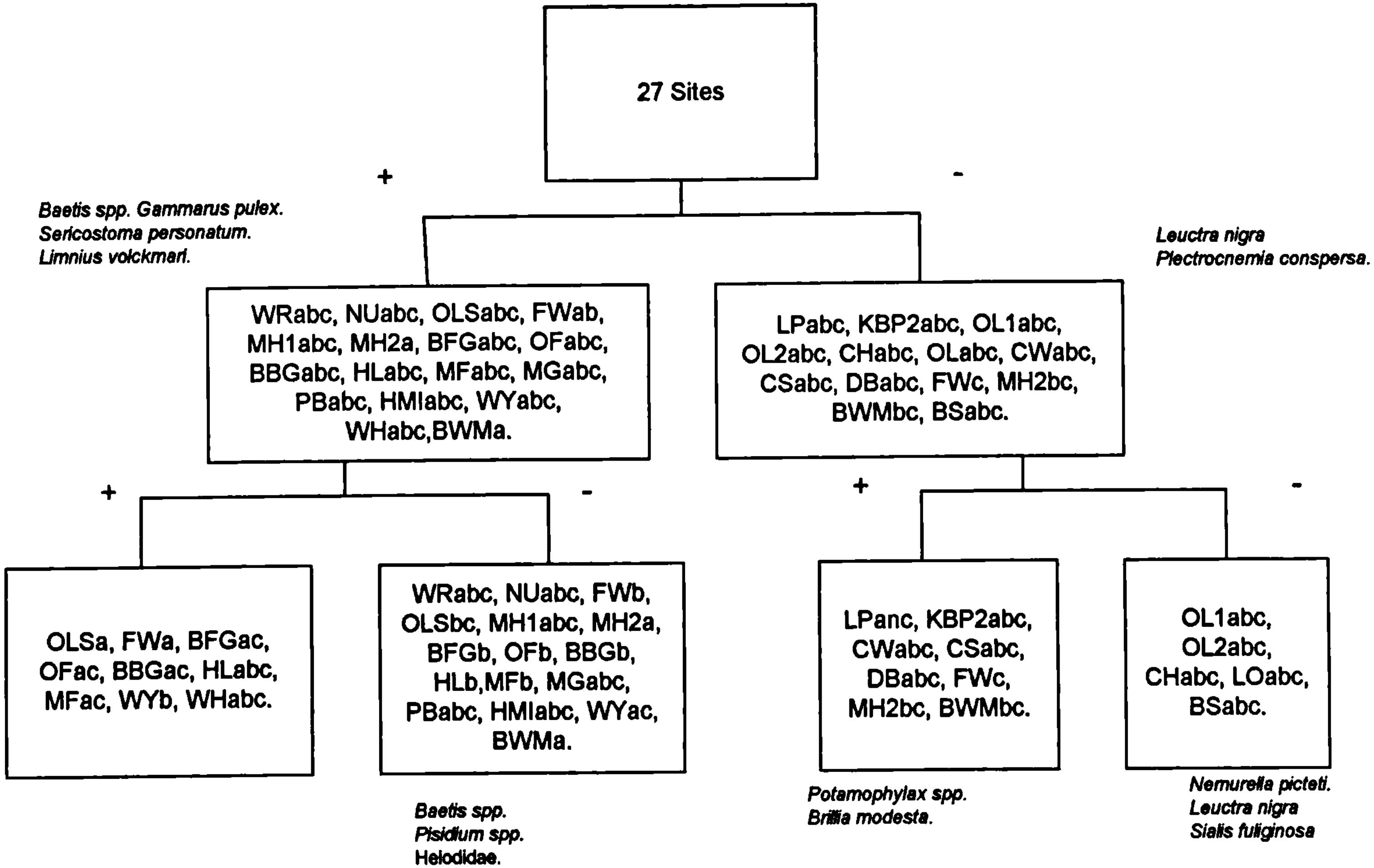


Fig 4.6: Classification of twenty-seven stream communities using TWINSPAN. Suffix a = 1976, suffix b = 1984 and suffic c = 1989. Indicator species are listed beside groups. Classification is taken to two levels only. The first division is on the basis of pH with circumneutral sites on the left (+) and acid to the right (-).

Table 4.7 shows that multiple discriminant analysis was successful in the prediction of the sites to the correct TWINSPAN grouping using the environmental variables of mean, minimum and maximum pH, summer temperature, conductivity, distance from source and discharge.

Table 4.7: The percentage of sites predicted to the correct TWINSPAN grouping using multiple discriminant analysis.

	TWINSPAN LEVEL	
	1	2
Number of significant discriminant functions ($P < 0.05$).	2	3
% of correct predictions.	83.2	76.0
% of sites in which correct group is the second most probable.	16.8	24.0

Although Canonical Analysis was carried out for all sites, a subset of the data only is presented in Table 4.8. This is because of the sheer number of data points indicating species and sites, which obscure the picture. A set of five acid and five circumneutral sites were chosen from the total data set and plotted for axes 1 and 2. The black spots are species and a few have lower case letters to indicate representatives. The upper case letters refer to sites: first, OL1, OL2, CH, LO and BS, are acid sites (original site numbers 6, 7, 8, 9 and 35, respectively); second, sites MF, MG, PB, HMI and WH (site numbers 25, 26, 27, 28 and 29, respectively) are circumneutral.Environmental variables are indicated with black arrows and include pH, temperature, distance from source, conductivity and discharge. The length of the arrow is an indicator of the strength of the association and, here, pH has the strongest association. Species tolerant of acid conditions and acid sites lie close to this line.

The strength of environmental variables can be examined by running a constrained CCA (ter Braak 1988) on each of the eight environmental variables (Table 4.8). In this type of analysis there is one constrained axis related to the environmental variable considered and a series of unconstrained axes. The correlation matrix table (Table 4.8), indicates that correlations are strong among many of the environmental variables, particularly pH and temperature.

Table 4.8: Weighted correlation matrix for environmental variables (weight = sample total), used in canonical correspondence analysis.

mean pH	1.000							
min pH	-0.906	1.000						
Max pH	-0.975	-0.949	1.000					
mean Temp	0.611	0.584	-0.596	1.000				
July Temp	-0.770	-0.705	0.748	0.665	1.000			
conductivity	0.785	-0.750	0.772	0.594	0.576	1.000		
discharge	0.623	-0.533	0.578	-0.749	-0.719	0.518	1.000	
distance	-0.479	-0.355	0.405	0.682	0.655	-0.386	0.946	1.000
	mean pH	min pH	max pH	mean T	July T	cond	disch	dist

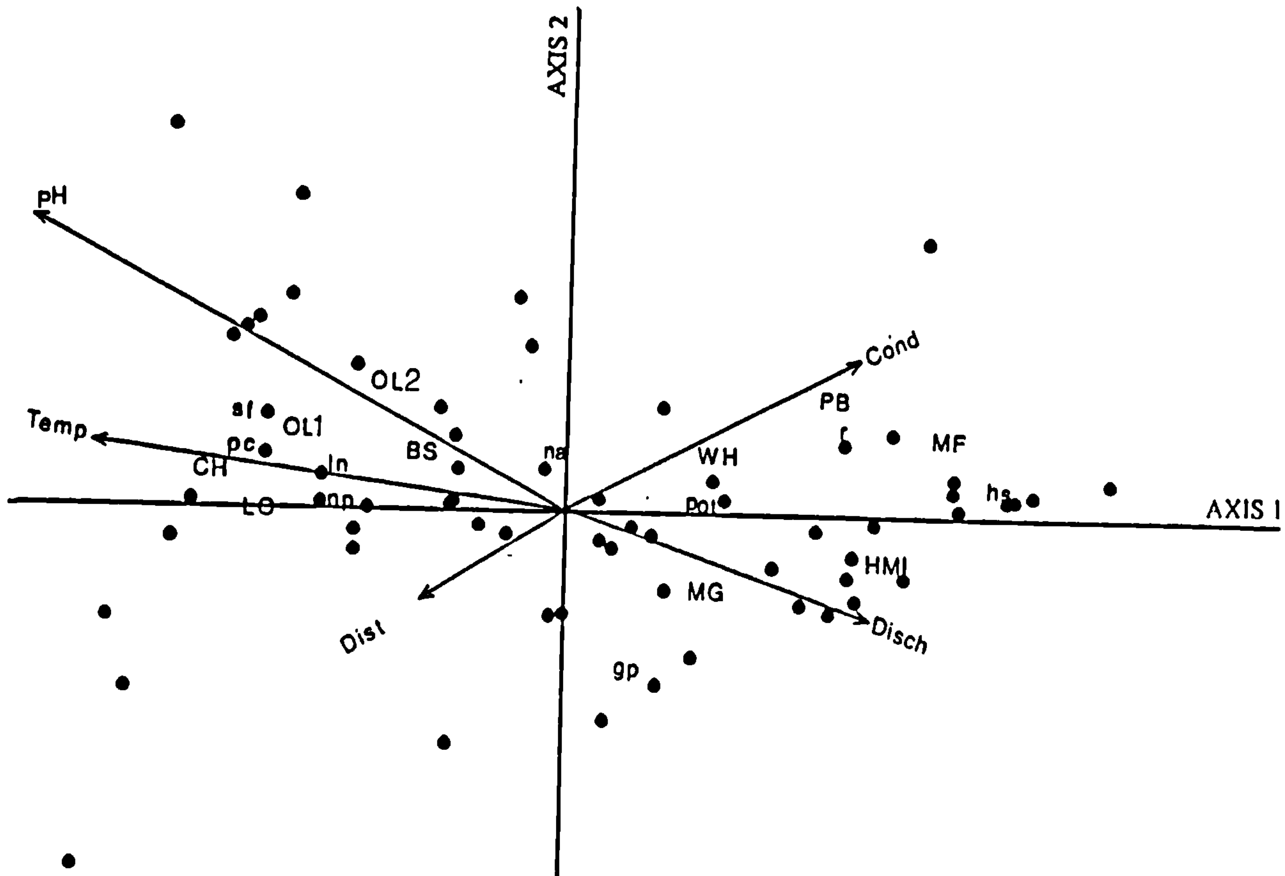


Fig 4.7: Plot of CANOCO, axes 1& 2 of a subset of the 1989 data. Due to large numbers of sites and species it was difficult to decipher the Canoplot so ten sites, five acid and five circumneutral, were chosen as being representative. These are plotted above. The data points refer to species and , where labelled are given lower case letters. Sites are indicated by upper case initials and arrows indicate environmental variables, the longer the arrow the greater the strength of association. All five of the acid sites fall out on the left of the graph and are associated with the environmental arrow for pH on axis 1. Species associated with axis 1 include, *Niphargus aquilex (na), Leuctra nigra (ln), Plectrocnemia conspersa* (pc), *Sialis fuliginosa* (sf) and *Nemurella pictetii* (np). Species associated with the circumneutral sites include, *Gammarus pulex* (gp), *Potamophylax* (pot), *Hydropsyche siltalai* (hs) and *Rhyacophila* (r).

4.vii. DISCUSSION

There is a broad agreement with the previous examination of community persistence for the Ashdown Forest streams (Townsend *et al* 1987). Having added extra replicates in time the data base has been expanded and the same general patterns are revealed. For this study, raw data from the original data sets were used and reworked.
Other studies on macroinvertebrates using similar techniques include Furse *et al* (1984), Wright *et al* (1984) and Ormerod & Edwards (1987). They found similar factors were strongly correlated with the first axis of ordination (alkalinity in Furse *et al* (1984) and Wright *et al* (1984), and total hardness in Ormerod & Edwards (1987)). As with previous surveys of the Ashdown Forest (Townsend *et al* 1983 and Townsend *et al* 1987), pH was most strongly correlated with axis 1 of DECORANA and my results are remarkably similar.

All three sampling occasions have coincidentally followed unusually hot, dry summers, which one would expect to have an effect on species composition and abundance. The most 'persistent' sites were those with low pH, low summer temperatures and low discharge. Where differences have occurred since previous sampling programmes, these tended to be related to changes in land use. Lavender Platt, for instance, has seen a rise in the mean annual pH. This may be attributed to local agricultural practices, and the rise in minimum pH for Boringwheel Mill could be due to the fish farming now taking place in the lake upstream.

The present suite of low pH sites are all located in areas draining heath and woodland. They have more natural channels, with fallen wood, leaf packs, and flow heterogeneity, providing a variety of habitats and possible refugia. They are sites which are least likely to be disturbed. Townsend *et al* (1983) looked at 34 stream sites in the

Ashdown Forest and concluded that patterns of species distribution and community structure were strongly associated with differences in acidity. Looking at an index of species turnover, Townsend (1989), analysed two classes of taxa (those typical of acid sites and those typical of circumneutral sites). The number of taxa gained, the number of taxa lost and the total number of taxa collected on the first of two sampling occasions were calculated. It was found that, whereas invertebrate species typically associated with acid conditions were by definition common at acid sites, they were also present at low densities in circumneutral sites. In assessing the rates of turnover of species and the losses and gains over the two sampling occasions, it was concluded that the fluctuations were greater in the circumneutral, downstream sites. There are a number of possible reasons for this, including the fact that fish are generally absent in the acid sites. This is also the conclusion reached by Otto & Svensson (1983), who found that large predators were more abundant in acid streams in Sweden where fish were rare or absent, suggesting that shifts in predation strategies and pressures may also contribute to differences in diversity and composition of stream insects in waters of contrasting pH. Species composition in the acid streams of the Ashdown Forest, depicted in the TWINSPAN classification (Fig 4.6), show species physiologically tolerant of low pH, including the large invertebrate predators *Plectrocnemia conspersa* and *Sialis fuliginosa*. Although many of these species are also found in the circumneutral sites, they are present in smaller numbers. It is possible that these sites may contain a larger fraction of the local species pool.

The three surveys now cover a total of thirteen years, adding to the data base for the Ashdown Forest stream sites. The spatial patterns among sites revealed in the two previous surveys certainly appear to be robust, and the pattern of persistence among sites was repeated. The low pH sites, as seen in the ordination plots (DECORANA), consistently

have ordination scores of around 200 and 100 on axes 1 and 2, respectively. In addition, a newer method of analysis (CANOCO), allows ordination of sites, species and variables together. The canoplot clearly illustrates that pH has the greatest influence on community structure showing the close relationship it has with certain species and sites.
The consistent relationship between physico-chemical factors and communities, between years, strengthens confidence that an environmental change, particularly in pH, would be detected by assessment of benthic communities.

In this suite of sites we have seen that those streams which have 'persistent' communities are those close to source, with a low pH, low discharge and having low summer temperatures. They are stream sites with retentive channels providing possible flow refugia - and they remain remarkably stable over time (Hildrew *et al* 1991). Perturbations can be distiguished by their frequency and intensity, with frequent disturbances tending to be of low intensity affecting a small proportion of the habitat. Stream communities are subject to recurrent small scale disturbances and have a remarkably swift recovery. For example, following an episode of flooding and scouring, disturbed or denuded patches of stream bed can recolonise rapidly from surrounding patches or refugia (Hildrew & Giller 1994). Of course, if one moves downstream from these 'persistent' sites, changes in land use allow organics to enter the stream system, altering the chemistry, and the streams become more open and subject to anthropogenic factors. The width of the channel and mean discharge increases, and the increased flow will remove obstructions, reducing possible refugia. These sites do not exhibit the same degree of 'stability'.

This research has been analytical rather than experimental, so questions as to the "process-level" interactions, which require small scale experimental studies, still remain unanswered. The Ashdown Forest is restricted geologically and to assess how useful this suite of sites may be for biomonitoring one needs to look further afield, to sites geographically and geologically different but with low pH. Chapter 5 looks at a different suite of sites, meeting the above criteria.

CHAPTER 5.

COMMUNITY PERSISTENCE IN STREAMS OF DIFFERING GEOLOGY AND GEOGRAPHICAL LOCATION.

5.i. INTRODUCTION.

Acidification of inland waters has received much publicity in recent years, with widespread interest in 'acid rain' and its effects causing public concern. However, we should not forget that low pH precipitation is not a new phenomena. Palaeolimnological biomonitoring of lake sediments, extracting diatoms and plotting out species assemblages, indicates that the industrial revolution was a major contributor to lake acidification (Dixit *et al* 1989; Battarbee *et al* 1990). Records of 'acid rain' in Europe have been available for more than thirty years now, with maps drawn by Ehrlich *et al* (1977) showing the spread from 1956-1966. These suggest that the areas in northern Europe receiving rainfall with a pH of less than 4.0 in 1959 had quadrupled in size by 1966.

The biological effects of acid deposition on aquatic systems has been well documented (e.g., Hall *et al* 1988; Gorham 1987). Work by Okland & Okland (1986), suggested that acidification affected aquatic organisms directly through physiological changes wrought by increased H^+ concentrations and by increasing concentrations of trace metals to toxic levels. Indirect effects include the slow decomposition rates of cellulose which limits available food (Hildrew *et al* 1984), and the avoidance of acid streams by insects during oviposition (Sutcliffe & Carrick 1973). Although H^+ stress has a detrimental effect on species richness and possibly productivity, detection of acid pollution is not possible by the use of traditional macroinvertebrate biotic indices, which were developed to detect organic pollution. This is because acid tolerant taxa include, for example, the Plecoptera which score high in biotic indices.

Despite the difficulty in linking acidification and invertebrate distribution patterns, several species and groups are recognised as sensitive to increases in acidity. Not surprisingly, animals requiring high calcium concentrations are likely to be rare. These include Crustacea and Mollusca (except for the Sphaeriidae). Lingdell & Engblom (1990) classified 3,631 Swedish lakes and streams using macroinvertebrates. Taxa classified as sensitive to acidification were found at approximately 60% (n = 2,167) of the sites sampled and, at 24% of the sites (n = 922), only acid-tolerant taxa were collected. Raddum & Fjellheim (1984), listed several taxa that they use as acid stress indicators in streams in western Norway. The order Ephemeroptera were the most sensitive group of insects with only 12 out of 34 species in the local species pool found at pH < 4.7, and with the majority of species disappearing from natural waters where pH fell below 5.0. A classification scheme based on their work is included in the International Co-operative Programme on the Assessment and Monitoring of Acidification of Lakes and Rivers (Anonymous 1987). As a general rule baetid mayflies are considered intolerant, whereas *Leptophlebia marginata* and *L. vespertina* are tolerant of low pH. However, there is some doubt about the use of *Baetis rhodani* as an early warning indicator of acidification, as suggested by Fjellheim & Raddum (1990), because it has been found in streams at pH <4.7 (Engblom & Lingdell 1983). Other groups known to be tolerant of acidification include certain species of Plecoptera, Trichoptera, Coleoptera, Megaloptera and Odonata, and some have been recorded as increasing their numbers in acid waters; which appears to be particularly true of those taxa no longer under predation pressure (Okland & Okland 1986).

A possible secondary effect of acidification is an increase in soluble aluminium ions resulting from acid leaching of soils and aquatic sediments. Generally, insects are less sensitive to trace metals - though toxicity levels are difficult to assess, particularly in conjunction with other metallic elements and under different environmental conditions. Because trace metal sensitivity is often related to life history features, such as size, feeding behaviour and development stage, it is difficult to obtain species-specific tolerance levels (Wiederholm 1984).

Sweden, with 20% of its total surface area affected by acidification (Lingdell & Engblom 1990), made an early start in monitoring its aquatic ecosystems. In addition, North American studies have looked at the effects of acidification, particularly on the fish stocks and fish yields of lakes (Oglesby 1977; Schindler *et al* 1985). Following a report by the United Kingdom Acid Waters Review Group (1988), it was recognised that in areas receiving drainage from catchments with base-poor rocks, particularly in the upland areas of northern and western Britain, there were waters which were acidic. A need for surveys comparable with those for acid waters in Scandinavia was recognised and a network of suitable sites was set up with funding from the Department of the Environment.

The United Kingdom Acid Waters Monitoring Network (UKAWMN) sites are distributed throughout the country, in the uplands of northern and western Britain as well as one site in the south-east of England, in the Ashdown Forest. These sites were chosen for the purpose of assessing the influence of projected changes in acid depositions on water quality, and they were specifically chosen to minimise the effects of anthropogenic catchment based impacts. The network consists of 23 sampling sites, eleven lakes and twelve streams, where regular spot sampling of chemical determinands are taken for analysis. In addition to water chemistry, diatoms, macrophytes, macroinvertebrates and fish are surveyed on an annual basis. For this study, only data from the twelve stream sites have been used. Sampling of benthic macroinvertebrates has been undertaken on an annual basis in the spring since 1988 and is intended to continue at least until 1997. Whereas the Ashdown Forest stream sites were confined to the same geographical and geological area, the UKAWMN sites are chosen for their susceptibility to acidification and come from disparate parts of the country. There have been two changes to the network since 1988 - Coney Glen was added in 1989 and Llyn Brianne was replaced by Afon Gwy in 1991. Using the same methods as those described in Chapter 4, I am looking to see if these communities also persist through time using four year's data and, if so, whether the same physico-chemical factors are associated with this persistence.

5.ii. METHODS.

Invertebrate Sampling.

Site names and grid references are given in Chapter 2. The sites consist of twelve streams which were sampled in the spring of each year begining in 1988. Llyn Brianne was replaced by Afon Gwy in 1991. Three one-minute kick samples were taken from riffle sections only, using a pond net, mesh size 330 um. A specimen reference collection is being compiled to ensure correct identification (as other research personnel will be identifying future samples). I collected samples in spring 1990, autumn 1990 and spring 1991. Details of geology and catchment are present in the site descriptions in Chapter 2, as is a map of the sites (Fig. 2.1).

Samples were preserved in the field using 4% Formaldehyde and hand sorted in the laboratory after sieving. Invertebrates were identified to species using a variety of taxonomic keys, excepting Chironomidae, Oligochaeta, Sphaeriidae and Hydracarina, which were not identified further. Counts were made and a species by site matrix compiled on a spreadsheet.

Environmental variables.

The methodology for collecting environmental data was determined by consultation and discussion within the Acid Waters Review Group. For the more stable chemical determinands analysis is carried out by the Institute of Hydrology. Local laboratories analyse determinands which require prompt analysis, and summaries of chemical data results are given in the annual Monitoring Network report (e.g. Juggins *et al* 1989). Flow and pH duration curves from continuously monitored stream sites are available from the Institute of Hydrology and the local laboratories.

Stable chemical determinands:

Determinand	Min. detection limit, ug	Method(s
Ca	50	ICP/OES
Mg	100	ICP/OES
Na	100	ICP/OES
K	750	ICP/OES
Ba	5	ICP/OES
Sr	1	ICP/OES
SO_4	100	Ion chromatography (Dionex)
Cl	100	Ion chromatography (Dionex)
Br	10	Ion chromatography (Dionex)
F	10	Ion chromatography (Dionex)
Cu	20	ICP/OES
Zn	20	ICP/OES
Fe	15	ICP/OES
Mn	2	ICP/OES
Si	80	ICP/OES
B	50	ICP/OES
Excess SO_4		Derived.

ICP/OES - Inductively Coupled Plasma / Optical Emission Spectroscopy.

A programme of Analytical Quality Control (AQC) is administered by the WRC.

Analytical methods of less stable chemical determinands from 'local' laboratories include pH using a Russell electrode, E.E.L pH meter or Radiometer. Conductivity was measured using a conductivity meter and alkalinity by Gran titration. Total oxidised N was obtained by Ion chromatography or colorimetrically, and PO_4 from Ion chromatography or spectrophotometrically. Aluminium was measured in three forms. Soluble non labile monomeric and soluble monomeric Al was obtained colorimetrically using Catechol or Pyrocatechol Violet, while soluble labile monomeric Al was derived by difference. Dissolved Organic Carbon was recorded using 'TOCSIN' Carbon Analyser, an Aqueous Carbon Analyser, a Technican Air Segmented Autoanalyser 11 or Colorimetrically (Copper Hydrazine Reduction).

Statistical analysis.

A matrix of species by site was compiled for the years 1988, 1989, 1990 and 1991. The means of the three samples were used and a Log_{10} x +1 transformation was confirmed using Bartlett's test. The same measures of persistence as were described in Chapter 4 were used. Multivariate techniques using the Fortran programes TWINSPAN, DECORANA and CANOCO were also used to analyse data and these were also described in Chapter 4.

5.iii. RESULTS.

5.iv. Physicochemical variables.

Physicochemical variables for each site are presented in Table 5.1. These are similar to the variables used in the Ashdown Forest survey: mean pH, pH range, temperature range, conductivity and catchment area. In addition, altitude range, wet deposition (acid) and wet deposition (sulphate) are included because these sites have been chosen for their susceptibility to acidification. Mean annual pH values range between 4.5 and 6.3. There is wider variation between sites for the other variables, as would be expected for sites from different geographical locations.

In Table 5.2 a matrix of Pearson's correlation coefficients between physicochemical variables is presented. The highest positive correlation was 0.67 between conductivity and minimum altitude with the relationship between rainfall and acid deposition and acid deposition and sulphate, at $r = 0.65$, a close second.

5.v. Measures of Persistence.

These are the same measures as those used for the Ashdown Forest stream sites. Table 5.3 gives measures of persistence for each UKAWMN site. Spearman's rank correlation coefficients, r_S, for Plecoptera alone are presented for data from 1990-91, for samples where the requirement of a minimum of seven pairs of measurements was met. There were less than seven pairs of measurements between years for two stream sites, the Bencrom River and Coney Glen. Pearson's product moment correlation coefficients between measures of persistence and six environmental variables are given in Table 5.4. Positive correlations are mostly between persistence measures and pH, and there are negative correlations between persistence measures and flow.

As previous work has shown pH is a significant factor closely associated with community persistence, Spearman's rank correlation coefficients and Sorenson's

SITE	Mean pH	pH Range	Temp range	Conductivity	Catchment area	Altitude range.	Mean rainfall	Wet dep. Acid	Wet dep. S
			^0C	$\mu S\ cm^{-1}$	ha	m	mm	kg H^+ $ha^{-1}yr^{-1}$	kg S $ha^{-1}yr^{-1}$
DL	5.6	4.6-6.9	4.0-12.5	35.1	210	260-716	2500	0.46	14.36
GB	5.3	5.0-5.7	4.0-13.0	34.1	210	260-712	2500	0.46	14.36
OL	4.5	4.1-4.7	5.7-14.7	95.5	240	94 -198	800	0.10	4.99
AH	5.4	4.3-7.8	4.4-9.5	38.6	358	355-690	2500	0.27	7.54
AAM	6.0	4.0-6.8	2.6-6.2	24.2	998	325-1111	1200	0.25	3.83
ACNC	5.8	4.1-6.5	4.5-9.8	40.0	790	10-756	2600	0.76	16.1
RE	4.8	3.8-6.0	2.0-12.0	82.3	1300	280-633	1600	0.64	16.8
NB	5.7	5.3-6.2	6.4-11.5	47.8	475	225-456	1800	0.25	6.35
BB	5.6	4.6-7.2	4.1-12.5	57.5	273	150-397	1400	0.13	11.4
BR	5.2	4.4-6.1	4.7-18.0	44.3	298	140-700	1700	0.25	12.51
CG	6.3	5.7-6.9	2.1-9.9	56.6	1414	230-562	1700	0.21	8.12
LB	5.8	4.6-6.7	1.0-8.0	40.3	77	330-450	1780	0.32	7.42

Table 5.1: Values of physicochemical variables from twelve stream sites from the United Kingdom Acid Waters Monitoring network (UKAWMN). Wet deposited non-marine sulphate data is included in the last column. Data is taken from 1988.

	Mean pH	Min pH	Max pH	Min Temp	Max Temp	Conductivity	Catchment	Altitude Min	Altitude Max	Rainfall	Acid Dep.	Sulphate
Mean pH	1	0.53*	0.66**	-0.35	0.64**	-0.33	0.22	0.04	0.48*	0.42	-0.12	-0.15
Min pH		1	0.14	0.05	0.07	-0.06	-0.04	0.12	-0.10	0.00	-0.19	-0.05
Max pH			1	-0.31	-0.52*	-0.37	0.10	0.01	0.49*	-0.68**	0.12	0.04
Min Temp				1	0.50*	0.03	-0.10	-0.26	-0.32	-0.07	-0.28	0.07
Max Temp					1	0.13	-0.30	-0.21	-0.43	-0.19	-0.15	0.47*
Conductivity						1	0.24	0.67**	-0.48*	-0.39	-0.34	-0.17
Catchment							1	0.09	0.38	0.13	0.21	0.00
Min Altitude								1	-0.9	-0.43	-0.34	-0.44
Max Altitude									1	0.38	0.65**	0.24
Rainfall										1	0.45	0.32
Acid Dep.											1	0.65*
Sulphate												1

Table 5.2: Matrix of Pearson correlation coefficients between physicochemical variables at twelve sites. Correlations significantly different from zero, *$p < 0.05$, ** $p < 0.01$.

SITE	JACC1	JACC2	JACC3	SOR1	SOR2	SOR3	SPR1	SPR2	SPR3	SPR4	SPR5	SPR6	SPRPLEC (1990-91)
DL	0.47	0.50	0.42	0.57	0.69	0.86	0.64	0.59	0.52	0.83	0.77	0.71	0.87
GB	0.48	0.53	0.38	0.69	0.58	0.78	0.62	0.67	0.78	0.51	0.62	0.68	0.97
OL	0.53	0.54	0.56	0.62	0.58	0.77	0.37	0.39	0.25	0.59	0.38	0.57	0.81
AH	0.55	0.57	0.41	0.61	0.64	0.72	0.72	0.57	0.66	0.66	0.85	0.65	0.94
AAM	0.74	0.50	0.64	0.79	0.54	0.62	0.67	0.49	0.52	0.47	0.39	0.37	0.69
ACNC	0.52	0.68	0.60	0.66	0.53	0.67	0.71	0.63	0.69	0.76	0.74	0.66	0.15
RE	0.50	0.63	0.47	0.51	0.56	0.77	0.60	0.63	0.66	0.73	0.60	0.56	0.77
NB	0.53	0.91	0.65	0.76	0.65	0.83	0.71	0.67	0.62	0.74	0.58	0.56	0.84
BB	0.50	0.39	0.53	0.49	0.50	0.66	0.57	0.69	0.54	0.45	0.49	0.51	0.57
BR	0.61	0.40	0.69	0.52	0.51	0.67	0.74	0.66	0.75	0.60	0.67	0.67	-
CG	-	0.33	-	-	0.46	-	-	-	-	0.49	0.44	0.60	-
LB	0.62	0.60	0.58	0.63	0.56	0.67	0.79	0.76	0.72	-	-	-	0.96

Table 5.3: Measures of community persistence. Derived from twelve stream invertebrate communities.
Key: JACC, Jaccard's index of similarity in community composition; SOR, Sorenson's index of similarity;
SPR, Spearman's rank correlation coefficient calculated for the complete community; SPRPLEC is the Spearman's r for Plecoptera. Numbers 1-6 are the years. 1 = 1988-89, 2 = 1988-90, 3 = 1988-91, 4 = 1989-90, 5 = 1909-91 and 6 = 1990-91.

indices are plotted against mean pH in Fig. 5.1. The lowest Spearman's r is for Old Lodge (Ashdown Sands), which was somewhat surprising as Old Lodge had a high correlation coefficient in previous survey data as was seen in Chapter 4. It is possible that the difference may be due to the different sampling methods (kick sampling rather than Surber sampling) and/or to the difference in collecting season (spring rather than autumn), or to chance. However, Sorenson's index for Old Lodge, for the three comparisons is high.

Fig 5.2 plots Spearman's r (a measure of persistence in rank abundance) against rainfall and acid deposition. Correlation coefficients were significant ($p<0.5$) for all sites except Old Lodge. Again, we see that the stream site from the Ashdown Forest appears to have a low persistence measure, whereas in Chapter 4 there is evidence to the contrary. Old Lodge lies in the bottom far left hand corner of the graphs and has the lowest pH, lowest rainfall and, apart from 1990, the lowest acid deposition. Only between the years 1988-91 does Old Lodge have a Spearman's *r* above 0.6. In Fig. 5.3, Spearman's *r* for Plecoptera is plotted against mean pH, mean annual temperature, conductivity and flow for the years 1990-91. Not all sites had enough species to allow pairs of measurements between two sampling occasions. For instance, Bencrom River and Coney Glen are missing, and so, to avoid confusion, all sites in Fig 5.3 are labelled with their initials. The rank abundance of Plecoptera at all sites is consistent between years (1990-91) except for Alt Coire nan Con. This site has a low mean annual temperature (as does Alt a' Mharcaidh). Only the Plecoptera at Alt Coire nan Con have a low Spearman's *r* - results from the total community give a Spearman's *r* greater than 0.6.

A frequency histogram of Spearman's r for the total community between the years 1988-89 (a), 1989-90 (b), 1990-91 (c), 1988-91 (d), 1989-91 (e) and 1990-91 (f), is given in Fig.5.4. Again, Old Lodge (marked with an asterisk), is the only site that does not have a significant Spearman's r.

Measure of Persistence	Mean pH	Min pH	Mean Temp	Conductivity	Discharge	Al	Rainfall	Acid Deposition	Sulphate
SPR 1	0.91**	0.87**	-0.93**	-0.94**	0.03	0.55*	0.96**	0.68**	0.65**
SPR 2	0.65**	0.98**	-0.79**	-0.81**	0.10	0.36	0.81**	0.60*	-0.75**
SPR 3	0.97**	0.57*	-0.88**	-0.87**	0.23	0.33	0.89**	0.75**	-0.19
SPR 4	0.05	0.69**	-0.28	-0.29	0.16	-0.03	0.28	0.25	-0.53*
SPR 5	0.78**	0.93**	-0.85**	-0.87**	-0.05	0.57*	0.89**	0.58*	-0.79**
SPR 6	0.86**	0.90**	-0.95**	-0.94**	0.62*	-0.07	0.92**	0.96**	-0.23
JACC 1	-0.39	0.37	0.48*	0.45	-0.99**	0.76**	-0.39	-0.81**	-0.50*
JACC 2	-0.05	-0.28	0.21	0.18	-0.91**	0.86**	-0.12	-0.56*	-0.46
JACC 3	-0.10	0.77**	0.98**	0.95**	-0.34	-0.26	-0.98**	-0.87**	0.29
SOR 1	0.27	-0.43	-0.05	-0.03	0.14	-0.08	0.03	0.13	0.57*
SOR 2	-0.37	0.33	0.15	0.14	-0.04	-0.09	-0.15	-0.15	0.42
SOR 3	0.05	0.37	-0.23	-0.20	0.85**	-0.78**	0.14	0.54*	0.32
PLEC	-0.54*	0.0	0.44	0.40	-0.69**	0.43	-0.37	-0.65*	-0.64*

Table 5.4: Pearson product moment coefficient between measures of community persistence and physicochemical variables in the UKAWMN stream sites. (Coefficients significantly different from zero: *$p < 0.1$, $r = 0.47$; **$p < 0.005$, $r = 0.69$). SPR = Spearman's r for the total community; PLEC = Spearman's r for Plecoptera: JACC = Jaccard's coefficient of similarity & SOR = Sorenson's coefficient of similarity. Numbers 1-6 = 1988-89, 88-90, 88-91, 89-90, 89-91 and 90-91 respectively.

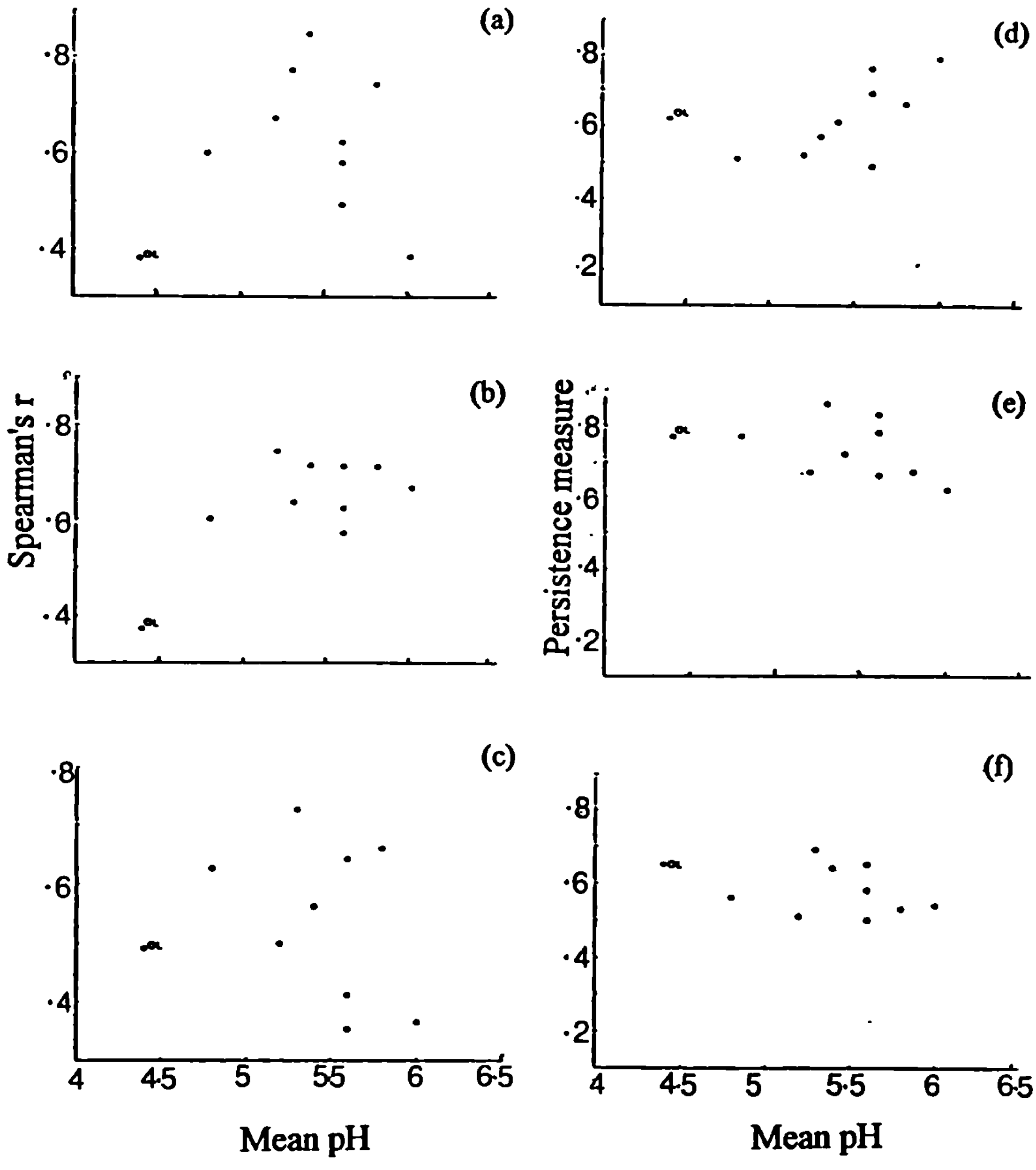


Fig. 5.1: Spearman's rank correlation coefficient for the total community are plotted against pH for 1988-89, 1988-90 and 1988-91 (a, b & c, respectively). Old Lodge is indicated by initials and is anomalous in having a Spearman's *r* below 0.4 for 1988-89 and 1988-90. Measures of persistence (Sorenson's index) are also plotted against pH between the same years (d, e & f, respectively) and here Old Lodge has a high measure of persistence. This site also has the lowest pH.

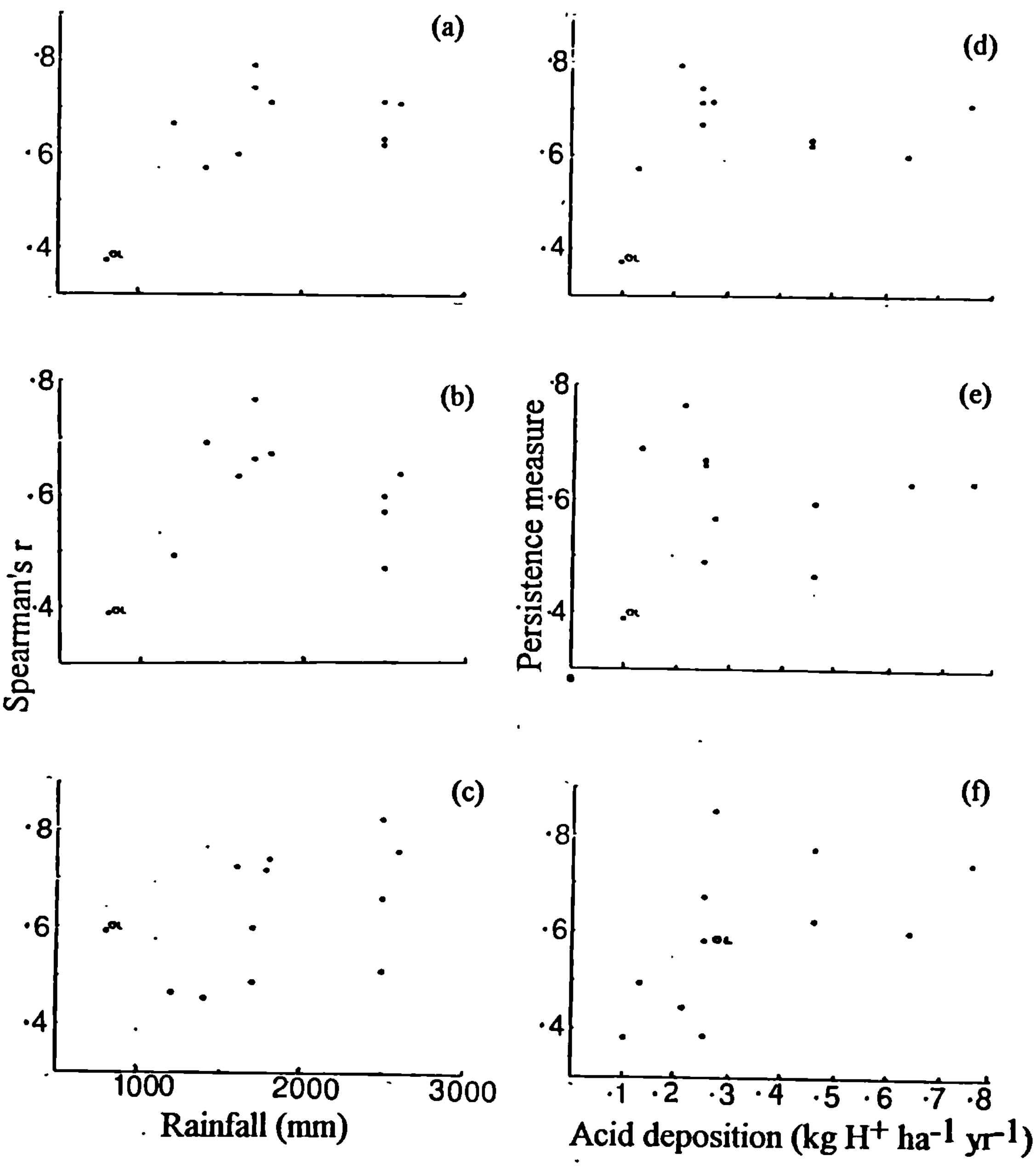


Fig. 5.2: Spearman's r (a measure of persistence in rank abundance) is plotted against annual rainfall (mm) and acid deposition between the years 1988-89, 1988-90 and 1988-91 (a, b & c, respectively for rainfall, and d, e & f, respectively for acid deposition). Again, Old Lodge has a low Spearman's *r* between 1988-89 and 1988-90 when this site also had the lowest rainfall and wet acid deposition. Between 1990-91 however, Old Lodge has a significant Spearman's *r* of 0.57.

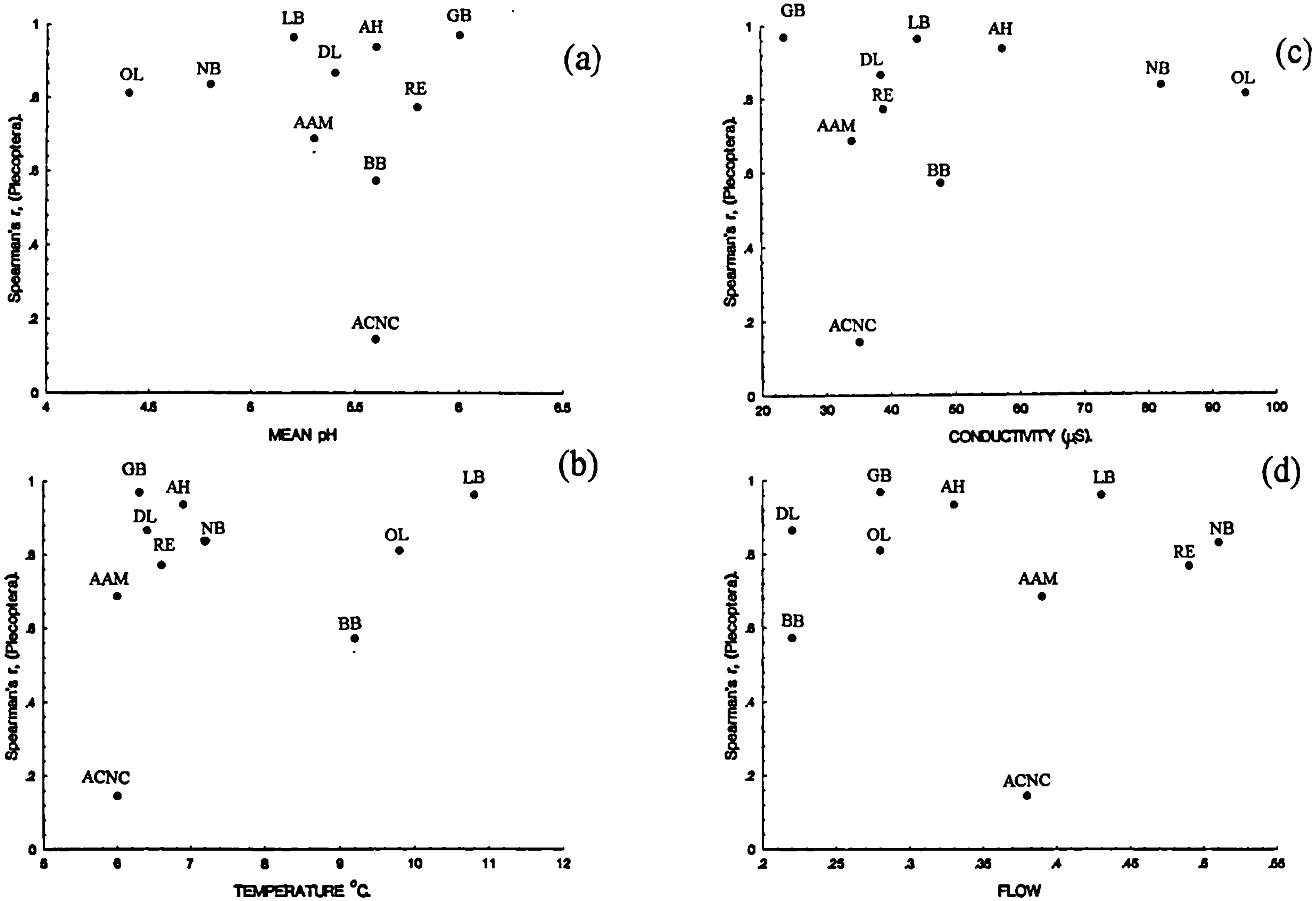


Fig. 5.3: Spearman's rank correlation coefficients for Plecoptera, for each of the UKAWMN sites plotted against different environmental variables. The data is from 1990-1991. As the Bencrom River and Coney Glen had less than seven pairs of measurements they are not included. Apart from Alt Coire Nan Con, all sites have significant results.

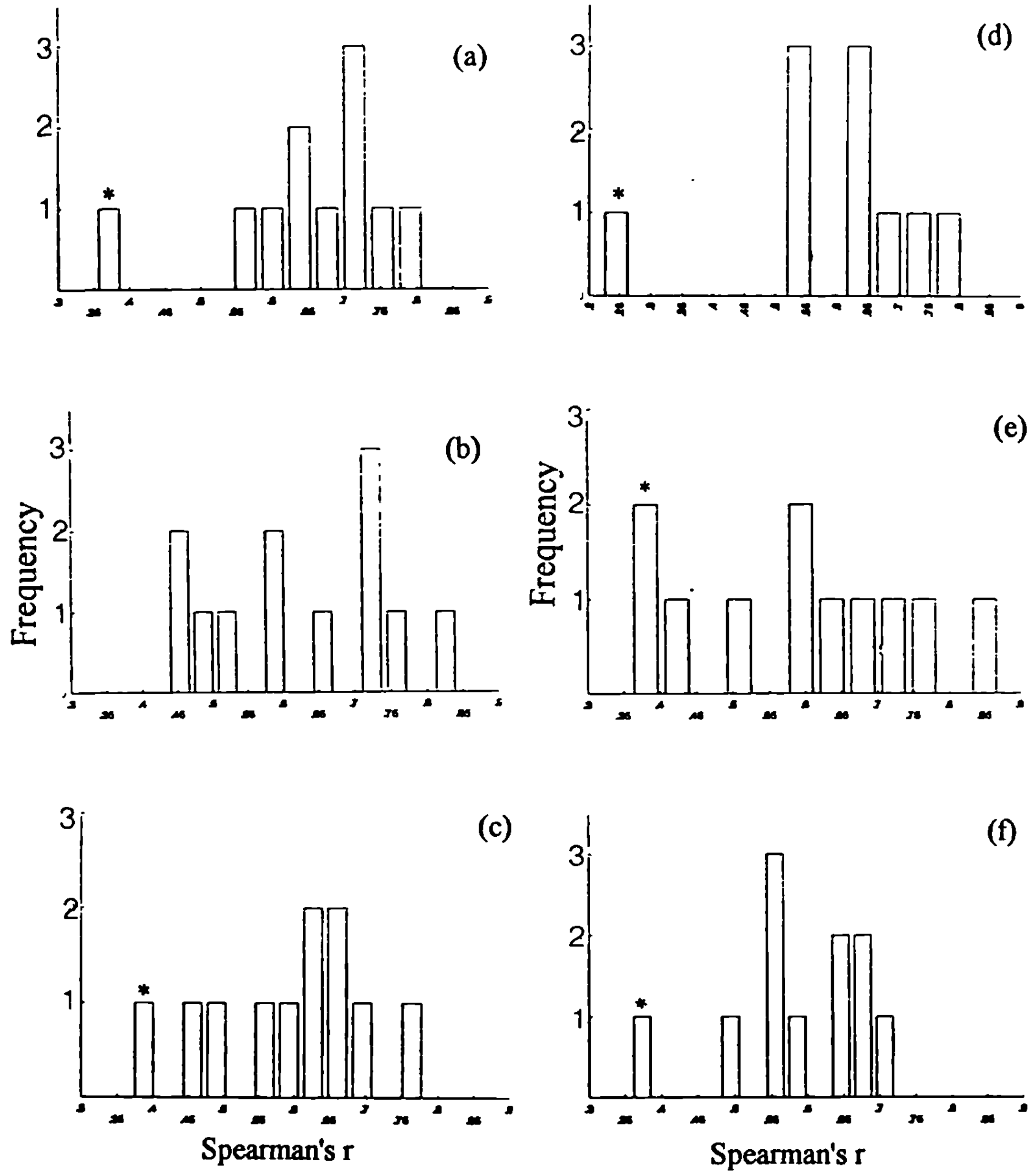


Fig. 5.4: Frequency distributions for Spearman's correlation coefficients between years 1988-89 (a), 1989-90 (b), 1990-91 (c),1988-91 (d), 1989-91 (e) and 1990 -91 (f). Old Lodge is the only site with a Spearman's *r* below 0.4(*).

5.vi. Spatial relationships.

The stream sites have been classified using TWINSPAN and ordinated for each of the four years, 1988-1991. As the term 'indicator' species does not relate to the prediction of species, they are listed for the year 1991 only (Fig 5.11).

Fig 5.5 gives the classification of sites for 1988 and Fig 5.6 gives the ordination using DECORANA. Stream sites were taken to three divisions and four groupings have been identified. These are marked with a bold capital letter and can be seen to correspond to the groupings in the ordination plot in Fig 5.6 where Old Lodge is an outlier. The first axis in the ordination is associated with temperature and the second axis with altitude. Fig 5.7 gives the Twinspan divisions for the year 1989. Again there are four groupings which correspond to the groups given in the DECORANA plot in Fig 5.8. In this figure Old Lodge is loosely associated with two other sites, Coney Glen and Narrator Brook. Axis one is associated with summer temperature and the second axis with altitude. The classification of sites for 1990 is presented in Fig 5.9. Again, TWINSPAN is taken to three divisions but five groupings were identified. In Fig 5.10, the ordination plot shows that once again Old Lodge is an outlier on axis 1. The first axis is most strongly correlated with pH and the second with summer temperature. The final year's data is given in Fig 5.11 as TWINSPAN groupings for 1991. Fig 5.12 gives the DECORANA plot and the five groupings, with Old Lodge again an outlier on the first axis. Table 5.5 shows the eigenvalues for each of the four axes produced by DECORANA for the years 1988-1991. In 1988, axes 1 and 2 between them account for 73.5 % of the variation of the data set and axis 1 alone accounts for 49.8%. For 1989 the percentage of variation explained by the first two axes is 79.5% and for 1990 it is 88.9% and, finally, in 1991 it is 81.2%.

In Table 5.6, Product-moment correlation coefficients between scores on DECORANA axes and environmental variables are given for 1989 only. These results were, however, consistent among years. Mean and maximum pH, maximum altitude, rainfall and acid deposition are all negatively correlated with axis 1, and maximum annual temperature is positively correlated with axis 1. For axis 2, minimum altitude is the only significantly and positively correlated variable, with rainfall and minimum temperature negatively correlated ($p < 0.05$).

The mean values of certain physico-chemical variables of the sites in each of the TWINSPAN groups for 1988 are plotted as histograms in Fig. 5.13. Groups A, B and C have mean pH values above 5.0, altitudes of more than 300 m and maximum summer temperatures below $13^{0}C$. All sites groups except D have conductivities below 60 uS cm^{-1}.

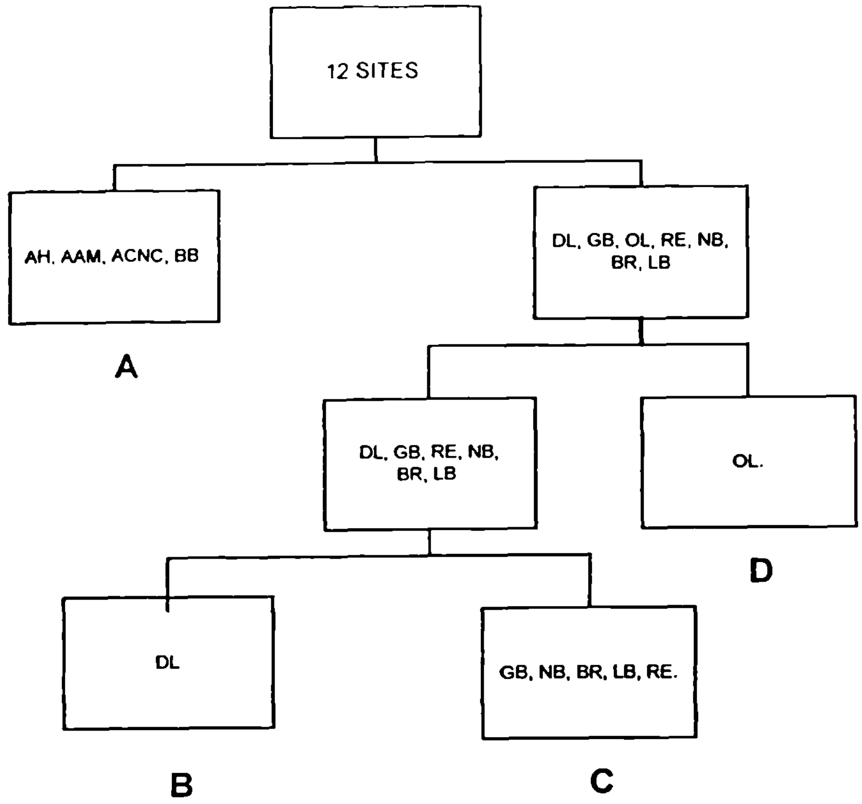


Fig. 5.5: TWINSPAN dendrogram for 1988. The sites are taken to three divisions. The capital letters relate to the detrended correspondence analysis below. (Coney Glen is not included as it was not added to the network until 1989).

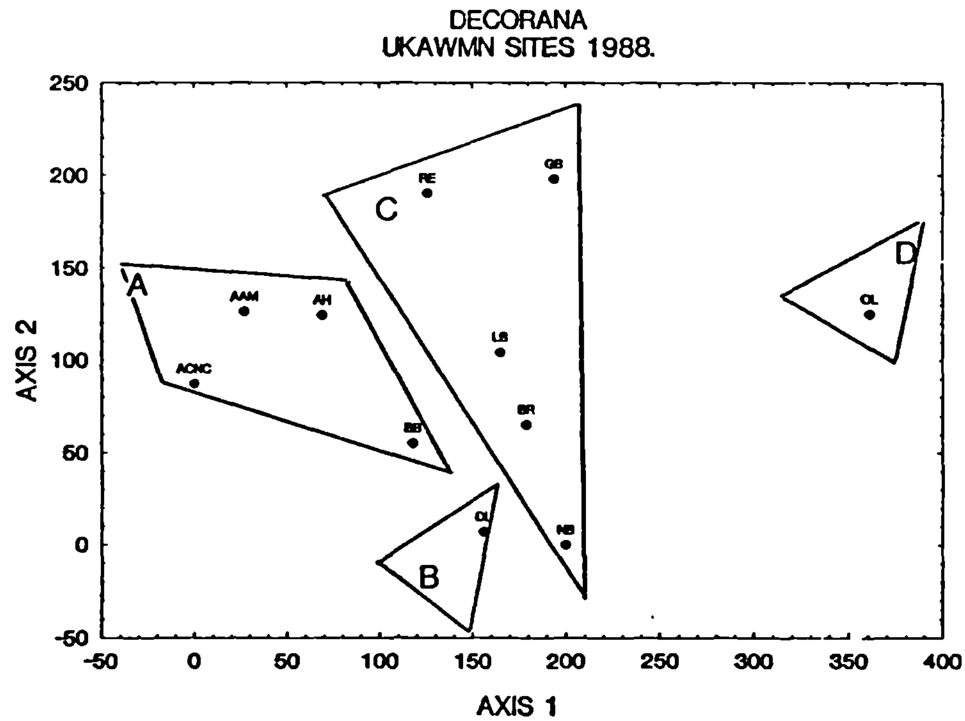


Fig. 5.6: DECORANA plot for 1988. Four groupings are identified which relate to the TWINSPAN divisions. The first axis is positively correlated with summer temperature and the second axis positively correlated with minimum altitude and negatively with rainfall.

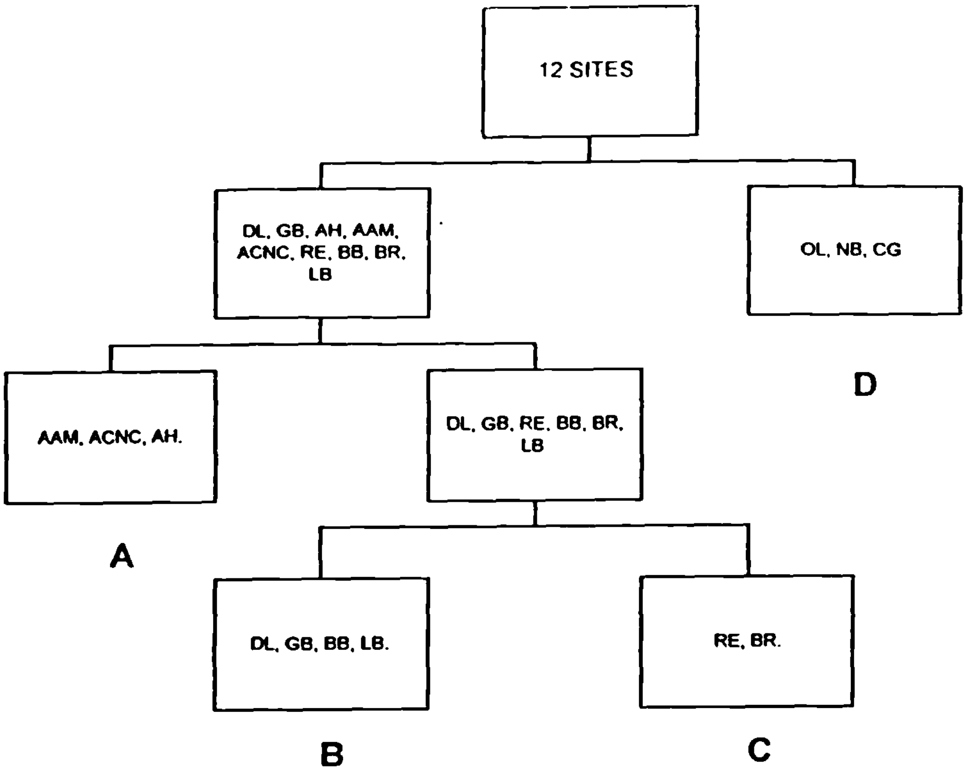


Fig 5.7: TWINSPAN groupings for 1989.

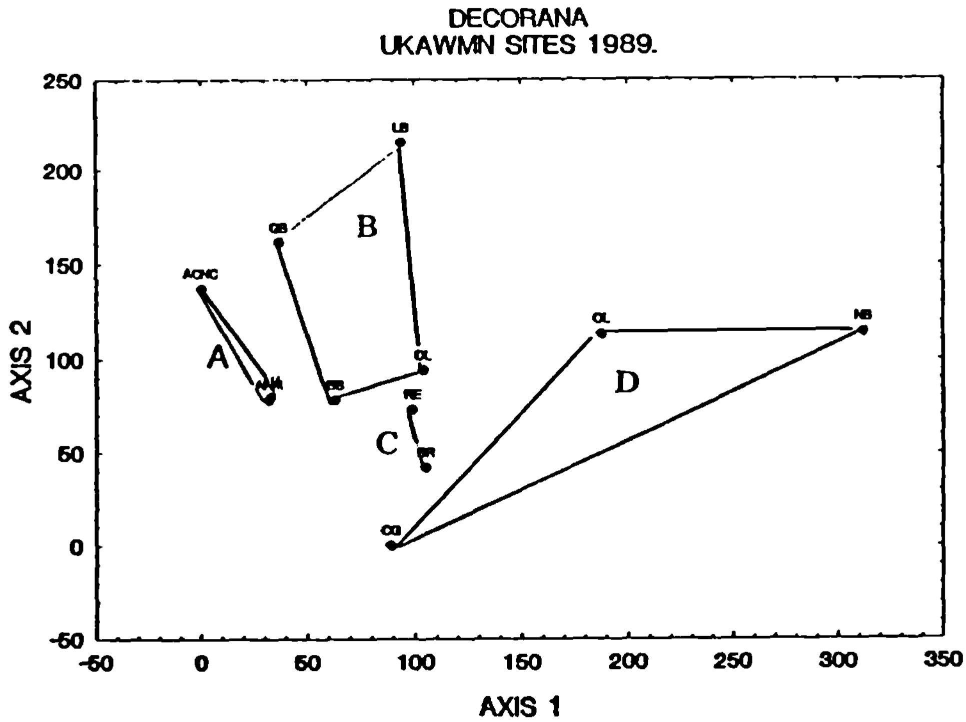


Fig 5.8: DECORANA plot for 1989. The first axis is positively correlated with summer temperature and negatively with maximum annual pH, maximum altitude and rainfall. The second axis is positively correlated with minimum altitude and negatively with minimum annual temperature.

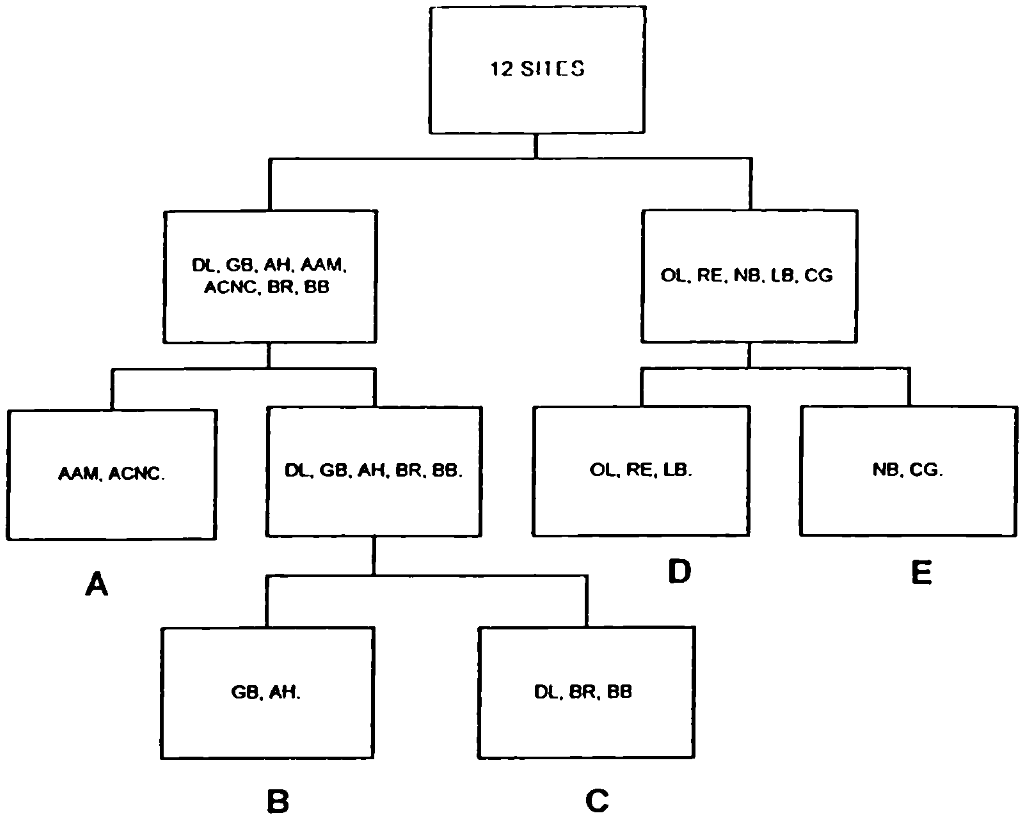


Fig. 5.9: TWINSPAN for 1990

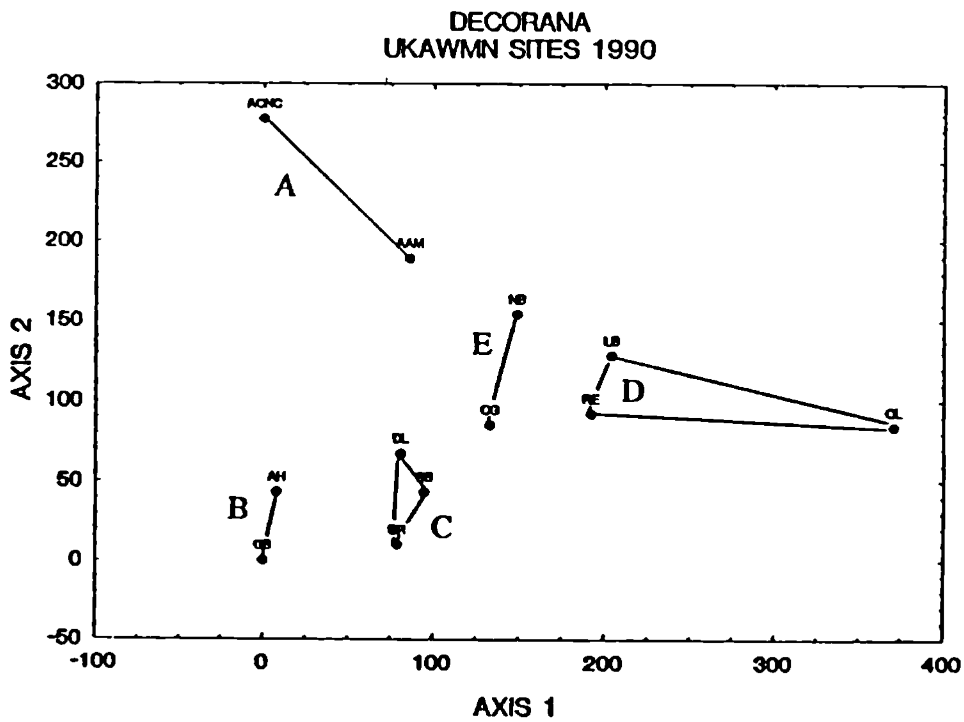


Fig. 5.10: DECORANA plot for 1990. The first axis most strongly relates to pH and the second axis to summer temperature. Old Lodge is an outlier on axis 1. The first two axes account for 88% of the variation with the first axis accounting for 62.3%.

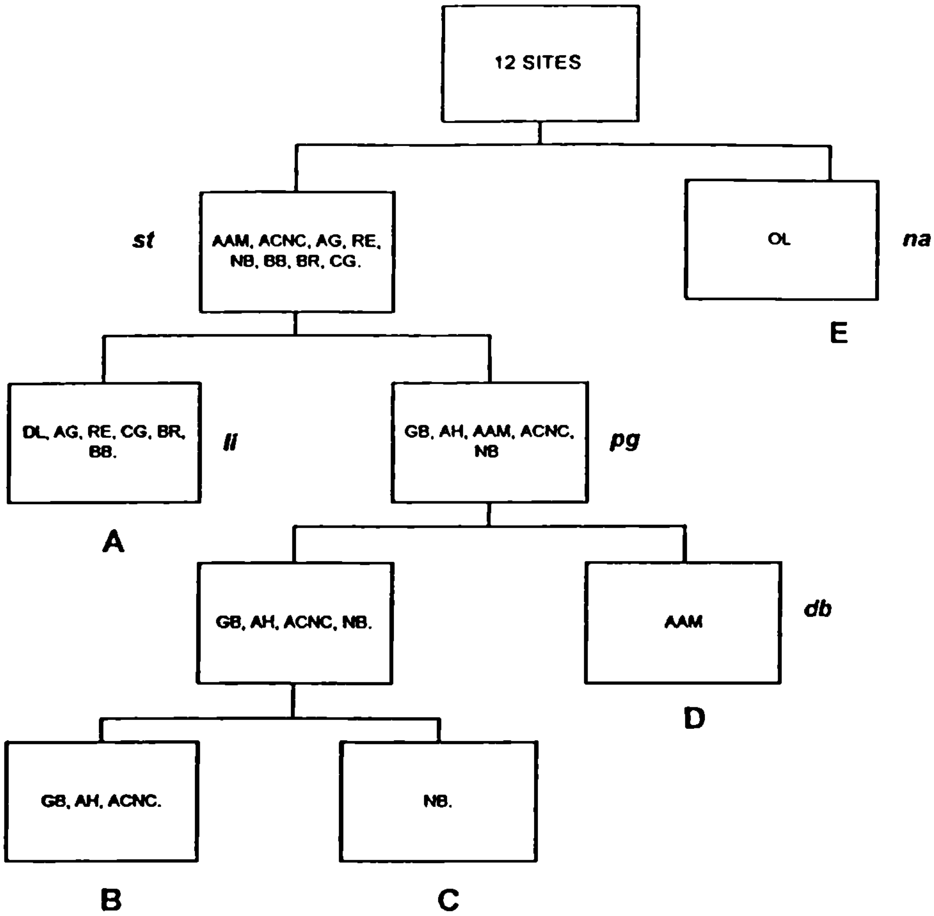


Fig. 5.11: TWINSPAN grouping for 1991. At the first level Old Lodge is separated from all the other sites and the species 'indicator' is *Niphargus aquilex*, which is only found at this site. The 'indicator' species for the other sites is *Siphonoperla torrentium*, which is associated with high flow conditions. Other 'indicator ' species listed are li = *Leuctra inermis*, pg = *Plectrocnemia geniculata* and db = *Diura bicaudata*.

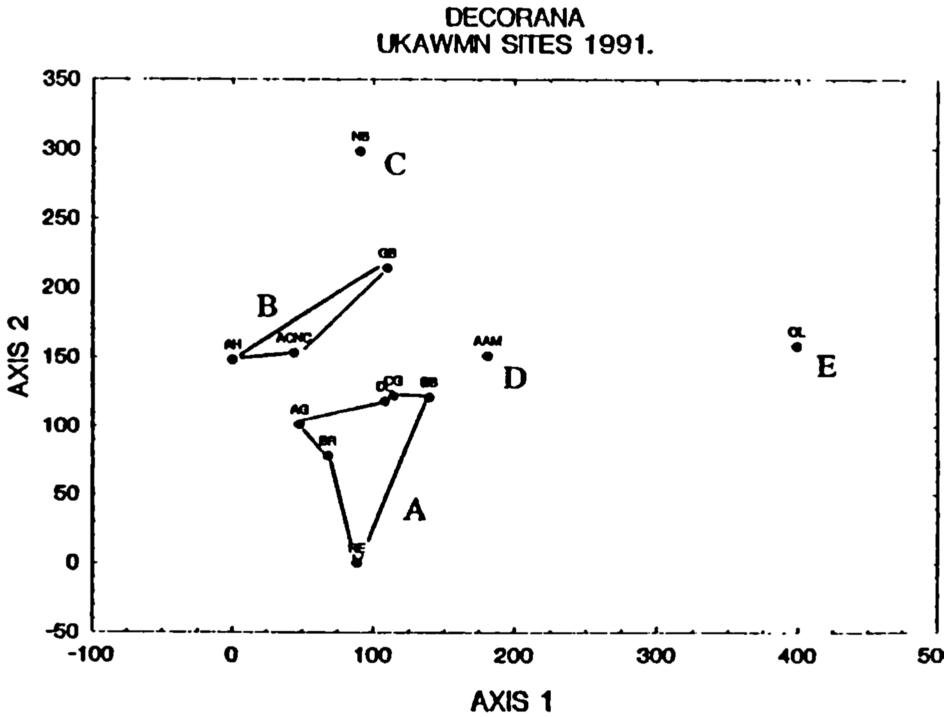


Fig. 5.12: DECORANA plot for 1991. Old Lodge is an outlier on axis 1 and Narrator Brook on axis 2. The first axis accounts for 53.8% of the variation and together the first two axes account for 81.2% of the variation.

Table 5.5 : Eigenvalues, percentage and cumulative percentage variance explained and lengths (in standard deviations) of DECORANA axes. 1988 - 1991 (a-d).

1988:(a)	Eigenvalues	% Variation Explained	% Cumulative Explained	Length (S.D.)
AXIS 1	0.544	49.8	49.8	2.36
AXIS 2	0.261	23.7	73.5	1.82
AXIS 3	0.112	13.6	87.1	1.43
AXIS 4	0.083	12.9	100	2.27

1989:(b)	Eigenvalue	% Variation Explained	% Cumulative Explained	Length (S.D.)
AXIS 1	0.516	54.1	54.1	2.33
AXIS 2	0.244	25.4	79.5	1.87
AXIS 3	0.18	18.9	98.4	1.45
AXIS 4	0.11	1.6	100	2.73

1990:(c)	Eigenvalue	% Variation Explained	% Cumulative Explained	Length (S.D.)
AXIS 1	0.619	62.3	62.3	2.14
AXIS 2	0.413	26.6	88.9	2.05
AXIS 3	0.187	7.1	96.0	1.74
AXIS 4	0.113	4.0	100	2.13

1991:(d)	Eigenvalue	% Variation Explained	% Cumulative Explained	Length (S.D.)
AXIS 1	0.567	53.8	53.8	2.34
AXIS 2	0.372	27.4	81.2	2.21
AXIS 3	0.203	12.9	94.1	1.54
AXIS 4	0.114	5.9	100	2.32

Table 5.6 : Product-moment correlation coefficients between scores on DECORANA Axes 1, 2 and 3 and environmental variables for 1989. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.005$.

	AXIS 1	AXIS 2	AXIS 3
Mean pH	-0.579*	-0.365	0.255
Min pH	0.256	-0.321	0.197
Max pH	-0.724***	-0.286	0.407
Min Temp	0.431	-0.501*	-0.146
Max Temp	0.674**	-0.130	-0.029
Conductivity	0.245	0.438	-0.606*
Catchment	-0.472	0.250	-0.417
Min Altitude	0.083	0.499*	-0.486*
Max Altitude	-0.790***	0.113	0.126
Rainfall	-0.583**	-0.516*	0.174
Acid Deposition	-0.542*	0.206	0.020
Sulphate	-0.198	0.071	0.221

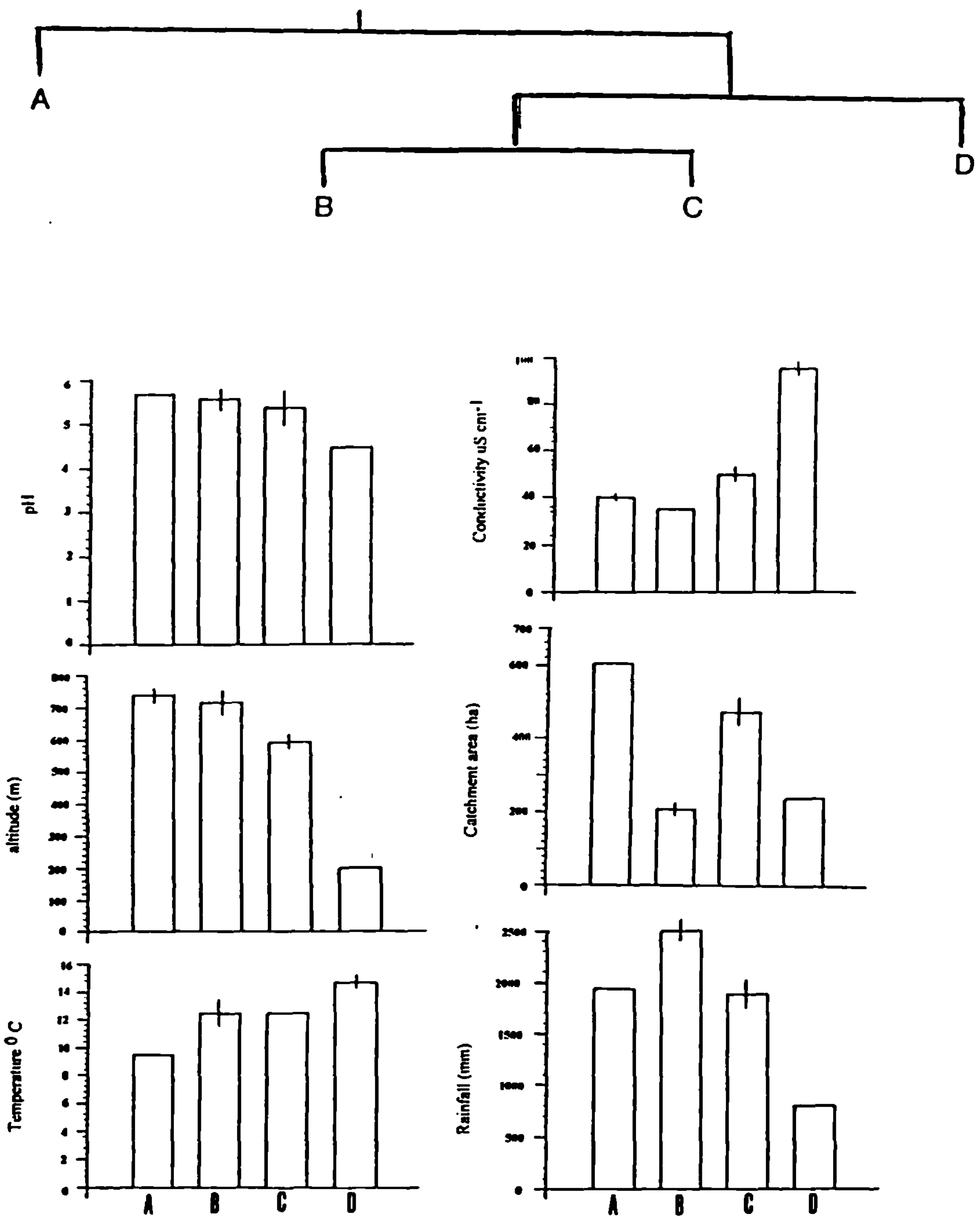


Fig. 5.13: The TWINSPAN groupings for 1988 are featured at the top of the figure as A, B, C & D. Six frequency distributions are given for each of the sites found within these groups for six environmental variables - letters at the bottom of each frequency distribution correspond to the TWINSPAN groupings. A, B & C all have pH greater than 5.0, altitude greater than 300m, maximum summer temperatures below $13^{0}C$ and D has conductivity below 60 $uS\ cm^{-1}$. The environmental variables are 1 = pH, 2 = altitude, 3 = temperature, 4 = conductivity, 5 = catchment area and 6 = mean annual rainfall.

Prediction of TWINSPAN groupings using Multiple Discriminant Analysis (MDA) is given in Table 5.7. The year 1989 is used as an example. The percentage of sites predicted to the correct group using MDA was high, with 90.1 % (level 1) and 54.3% (level 3) of the sites to the correct TWINSPAN grouping using pH, altitude, temperature, rainfall, conductivity, catchment area and flow (Table 5.7). The number of significant discriminant functions ($p < 0.05$) at each level of division are also shown, along with the percentage of sites for which the correct group was the second most probable as predicted by MDA.

Table 5.7: The percentage of sites predicted to the correct TWINSPAN group using MDA

	TWINSPAN LEVEL		
	1	2	3
Number of TWINSPAN groups.	2	3	4
Number of significant discriminant functions ($p<0.05$).	1	2	3
Percentage of correct predictions.	90.1	78.6	54.3
Percentage of sites in which the correct group is second most probable.	8.7	19.5	31.4

Canonical analyses for the years 1988-91 are presented in Figures 5.14 and 5.15. The analysis was carried out on eleven sites only for 1988, as site 22 (Coney Glen) was not included until 1989. For the other three years twelve sites were analysed. The sites are depicted by their initials in capital letters and underlined, and the species are represented by black dots. To avoid obscuring the picture, not every species data point is included, and only certain species are labelled, with their initials in lower case letters. See Table 5.8 for a listing of the species with their initials. Environmental variables are illustrated with black arrows and the length of the arrow is an indicator of the strength of association.

Table 5.8: Table of species and their initials.

Ameletus inopinatus	ai
Amphinemura sulcicollis	as
Anacaena globulus	ag
Brachyptera risi	br
Ceratopogonidae	cer
Cordulegaster boltoni	cb
Diura bicaudata	db
Drusus annulatus	dr
Ecdyonurus venosus	ev
Esolus parallelepidus	ep
Isoperla grammatica	ig
Leuctra hippopus	lh
Leuctra inermis	li
Leuctra nigra	ln
Limnephilidae	l
Limnius volckmari	lv
Nemoura cambrica	nc
Nemurella pictetii	np
Niphargus aquilex	na
Oreodytes sanmarkii	os
Oulimnius spp.	ou
Pedicia rivosa	pr
Perlodes microcephala	pm
Plectrocnemia conspersa	pc
Plectrocnemia geniculata	pg
Polycentropus flavomaculatus	pf
Polycentropus irroratus	pi
Potamophylax cingulatus	pc
Protonemura praecox	pp
Protonemura meyeri	pem
Rhyacophila dorsalis	rd
Rhithrogena semicolorata	rs
Rhithrogena spp.	r
Sialis fuliginosa	sf
Simuliidae	sim
Siphonoperla torrentium	st
Stenophylax spp.	s
Wormaldia spp.	w

There were 32 environmental variables included in the analysis. Of these only those with significant scores have been plotted.

Table 5.9: Table of eigenvalues for axes for each year and percentage of variance explained.

	Axis 1	Axis 2	Axis 3	Axis 4
1988	0.506	0.280	0.204	0.203
Var %	42.4	23.5	10.6	10.5
1989	0.507	0.328	0.210	0.113
Var %	43.8	28.3	18.1	9.7
1990	0.438	0.285	0.161	0.111
Var %	35.0	28.6	16.2	11.2
1991	0.410	0.327	0.213	0.236
Var %	34.6	27.6	17.9	19.9

For the year 1988, CCA axis 1 and axis 2 explained 42.4% and 23.5% respectively, of the variance in the species-environmental variable biplot and, for 1989, 43.8% and 28.3% . Table 5.9 gives the eigenvalues and the percentage variance explained for each axis for each year. The CANOCO plots for 1988 and 1989 are found in Fig. 5.14 a & b respectively. For 1988, [Cl] and [Ca] are most strongly correlated with axis 1 and pH and temperature with axis 2. For 1989, TON, flow and [Ca] are the variables most strongly correlated with axis 1, and Cl and temperature positively correlated with axis 2. Table 5.10 gives the weighted correlation matrix for the four years, showing the relationship between species axes and environmental variables.

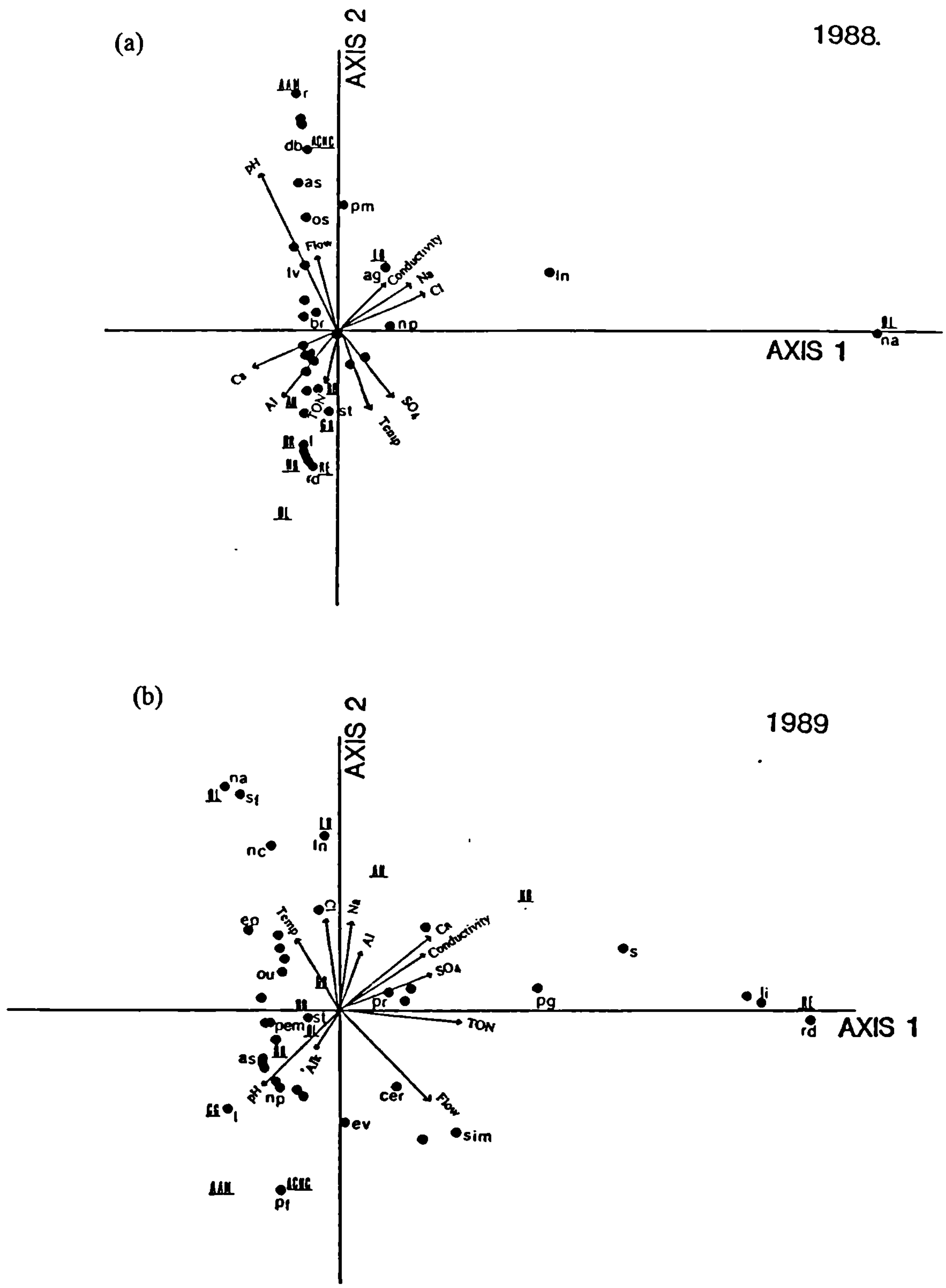


Fig. 5.14: CANOPLOTS for 1988 (a) and 1989 (b). The first axis is correlated with [Cl] and [Ca], and axis 2 with pH and temperature. For 1989, the first axis is correlated with TON and [Ca], and flow with axis 2. Each of the sites is plotted with capital letters, underlined, and each of the species is depicted by a black dot and lower case initials. The list of species names can be found in Table 5.8. Environmental variables are shown as arrows and the length of the arrow is an indiactor of the strength of association.

Table 5.10: Correlation matrix showing the relationship between species axes and environmental variables.

1988.

	Axis 1	Axis 2
Flow	-0.303	0.164
Temp	0.362	-0.513
pH	-0.503	0.533*
Alk	-0.433	0.510
Conductivity	0.509	-0.395
Ca	0.571*	-0.252
Mg	0.509	-0.409
SO_4	0.409	-0.351
TON	-0.073	-0.383
Cl	0.753**	-0.353
Al	-0.080	-0.089
Na	0.681*	-0.363

1989.

	Axis 1	Axis 2
Flow	0.579*	-0.629*
Temp	-0.180	0.542*
pH	-0.284	-0.440
Alk	-0.155	-0.243
Conductivity	0.490	0.625*
Ca	0.493	0.613*
Mg	0.408	0.623*
SO_4	0.446	0.424
TON	0.828**	-0.068
Cl	-0.086	0.599*
Al	0.146	0.440
Na	0.004	0.543*

1990.

	Axis 1	Axis 2
Flow	-0.385	-0.346
Temp	0.357	0.557*
pH	-0.651*	0.323
Alk	-0.484	0.490
Conductivity	0.385	-0.293
Ca	0.385	-0.319
Mg	0.384	-0.296
SO_4	0.344	-0.377
TON	-0.057	-0.312
Cl	0.405	0.055
Al	0.322	-0.117
Na	0.162	0.476

1991.

	Axis 1	Axis 2
Flow	-0.630*	0.532*
Temp	0.131	0.349
pH	-0.322	-0.811**
Alk	-0.367	-0.675*
Conductivity	-0.095	0.833**
Ca	-0.091	0.800**
Mg	-0.073	0.811**
SO_4	-0.027	0.857**
TON	-0.145	0.853**
Cl	0.072	0.454
Al	0.018	0.611*
Na	-0.043	0.506

In Fig. 5.15, the CANOPLOT for 1990 has pH as the variable most strongly correlated with axis 1 and temperature with axis 2. For the year 1991 the variable most strongly related to axis 1 is flow, and for axis 2, conductivity, SO_4 and TON; pH is negatively correlated with axis 2. For all four years the first two axes explain over 60% of the variation. The pattern of sites and species is not consistent for each year. For 1988 and 1990 site 13 (Old Lodge) is an outlier on axis 1, but for 1991 it is joined by site 23 (Green Burn). In 1989, site 12 (River Etherow) is the outlier on axis 1, but in other years is closely associated with axis 2. Old Lodge in 1989 is associated with axis 2, a reversal of other years.

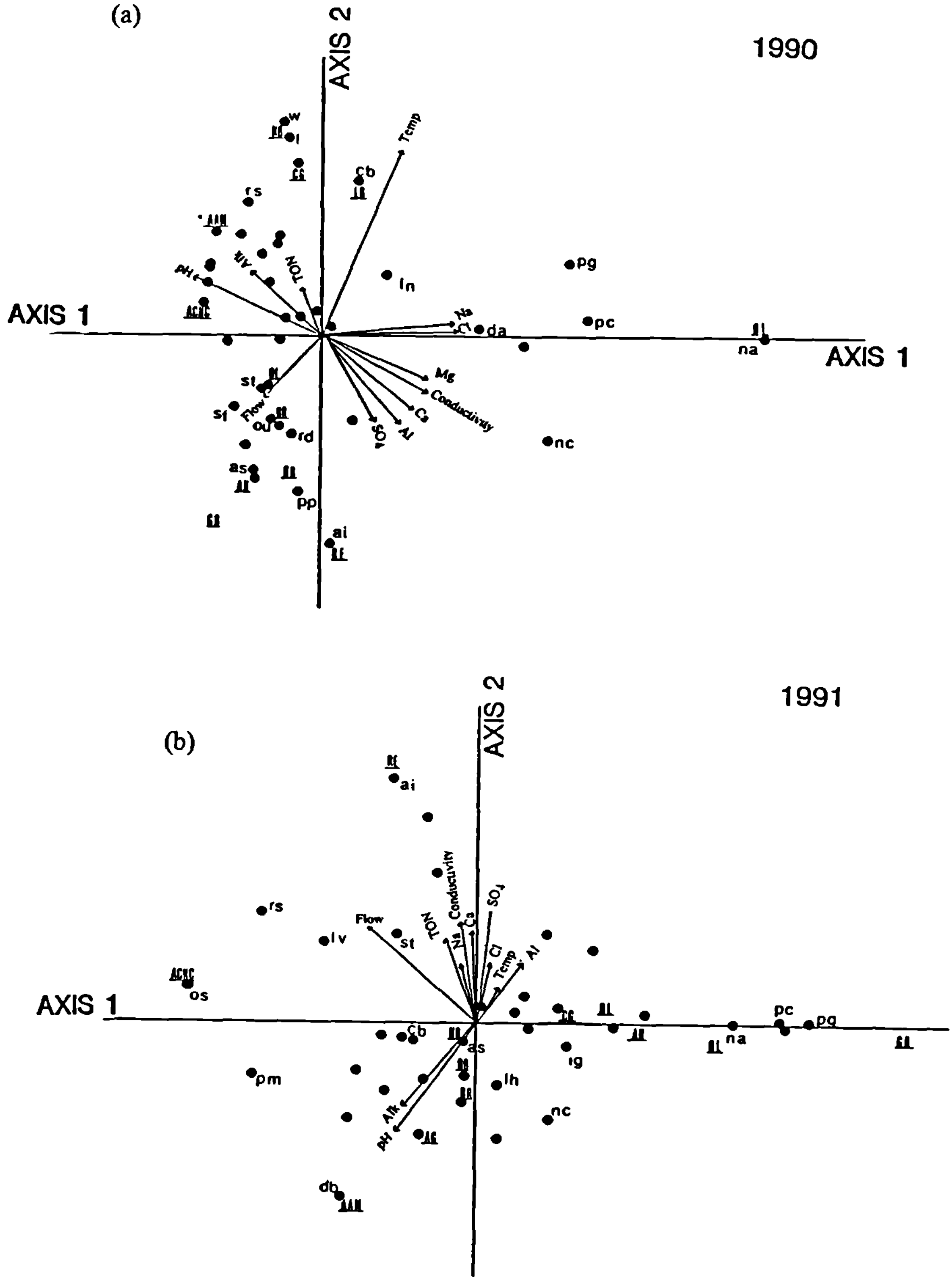


Fig. 5.15: CANOPLOTS for 1990 (a) and 1991 (b). In 1990 the variable most strongly associated with axis 1 is pH and for axis 2 it is temperature. For 1991, flow is most strongly associated with axis 1 and pH with axis 2. Sites are plotted as capital letters and underlined; species as black dots and lower case initials (species list in Table 5.8). Environmental variables are given as black arrows, the length of which indicates the strength of association.

The arrow for an environmental variable points in the direction of maximum change and variables with long arrows are more strongly correlated with the ordination axes and so more closely related to the pattern of community variation shown in the CANOPLOT.

It is sometimes helpful to extend the arrow in the opposite direction and then draw a perpendicular line from the species or sample scores to the arrow (ter Braak 1987). The intersecting point identifies the approximate weighted mean value of the specific environmental variable for each taxon or site. Fig. 5.16 gives an example using data from 1989. Flow is the variable most strongly associated with axis 2 and this variable arrow has been extended. It can be seen that taxon such as *Siphonoperla torrentium* and Simuliidae (st & sim respectively), which are invertebrates associated with high flow conditions, are closely linked with this environmental variable, (that is they fall closest to the line for flow).

Table 5.11: Weighted correlation matrix for environmental variables (weight = sample total), used in canonical correspondence analysis.

Flow	1.0											
Temp	0.556	1.0										
pH	-0.649	0.949	1.0									
Alk	-0.484	-0.007	0.895	1.0								
Cond	0.730	0.006	-0.645	-0.518	1.0							
Ca	0.684	0.263	-0.527	-0.318	0.945	1.0						
Mg	0.684	0.407	-0.680	-0.431	0.978	0.944	1.0					
Na	0.875	0.665	-0.643	-0.419	0.809	0.741	0.823	1.0				
TON	-0.057	0.166	-0.507	-0.308	0.479	0.364	0.454	0.016	1.0			
Cl	0.904	0.611	-0.527	-0.315	0.753	0.741	0.778	0.978	-0.103	1.0		
Al	0.644	0.557	-0.854	-0.645	0.614	0.466	0.579	0.549	0.575	0.473		
SO_4	0.542	0.278	-0.808	-0.664	0.885	0.805	0.802	0.529	0.693	0.447	0.693	1.0
	Flow	Temp	pH	Alk	Cond	Ca	Mg	Na	TON	Cl	Al	So4

The weighted canonical correlations are presented in Table 5.11. All variables are significantly correlated with pH and conductivity and, apart from TON, all variables are significantly correlated with flow.

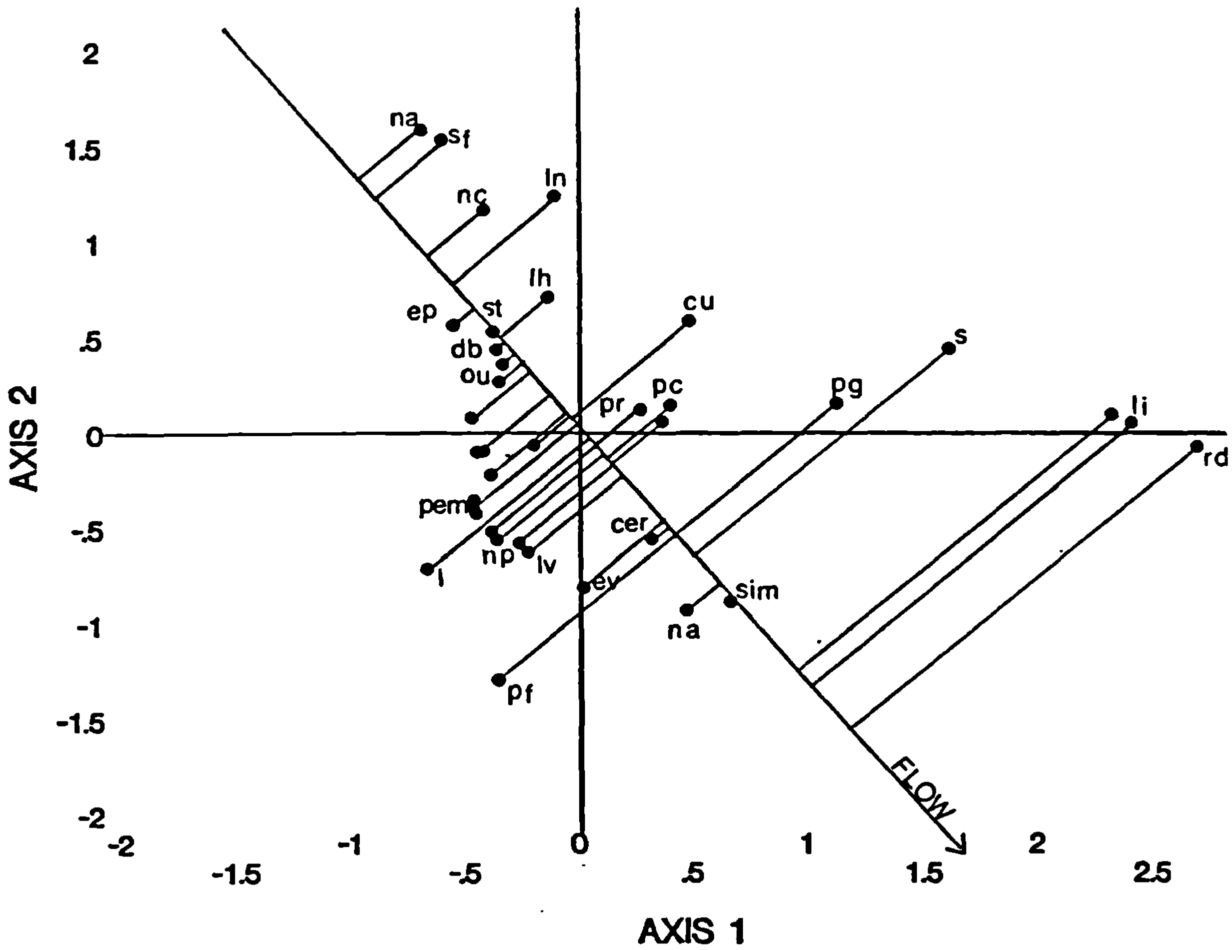


Fig. 5.16: CANOPLOT for 1989 with species and one major environmental variable plotted. Flow is highly correlated with axis 1 and the arrow has been extended. Perpendicular lines are drawn from the species to the arrow. The intersecting points identifies approximate weighted mean values of the specific environmental variable for each taxa. Here *Siphonoperla torrentium* and Simuliidae (st and sim) are most closely associated, as would be expected in high flow conditions.

5.vii DISCUSSION.

Although the measures of persistence are generally high, there are not the same clear-cut patterns emerging from one year to the next as were evident in the Ashdown Forest suite of stream sites (Chapter 4). The Spearman's rank correlation coefficients for the total community between all four years were significant except for site 13 (Old Lodge), although this site showed high persistence measures in the Ashdown Forest data set. Looking at a number of variables, Old Lodge was aberrant, having the lowest mean annual rainfall, wet acid deposition and mean pH of all the UKAWMN stream sites. The UKAWMN samples are collected from three kick samples, whereas the Ashdown Forest data is collected from five Surber samples and one possibility is that the samples were too small. For Plecoptera alone, site 3 (Allt na Coire nan Con) was the only site with a Spearman's r below 0.5. That is to say that the strength of association between any two years was consistent and, for all but one site, generally high. The two measures of similarity used, Jaccard's and Sorenson's, looked at similarity of species composition between years and again these were generally high. Sorenson's index, because of the way it is calculated, is always slightly higher than Jaccard's.

With regard to the multivariate analysis, the patterns were variable. This is not really surprising when we compare the acid Ashdown sites of Chapter 4 (which are constrained by geology, of a similar substrate type, close to source, and within decidious woodlands with narrow channels) to the UKAWMN sites. The UKAWMN sites have even less in common. Although low pH is important, it is evidently not the only variable differing among the twelve stream sites, (conductivity and [Al] are, of course, related). Channel width and flow rates are amongst the variables which vary greatly within the UKAWMN sites, as are substrate type and catchment. Persistence was generally high but does not vary consistently with pH, as it does in the Ashdown Forest data set (which includes the awkward case of Old Lodge). pH, nevertheless, is still the key variable associated with community structure.

The use of a direct gradient analysis like Canonical Correspondence Analysis, is valuable as it allows the probability of occurrence of populations along an environmental gradient to be inferred. Most methods currently available for direct gradient analysis allow for the analysis of one species at a time (ter Braak 1986). CCA comes into its own as it has the ability to analyse large number of taxa, simultaneously studying the effects of environmental variables. Weighted averaging indicates the centre (mode of the unimodal curve) of a species distribution along an environmental axis (ter Braak & Looman 1986). That is, a taxon may be more abundant close to its optimum (excluding factors such as predation), and weighted averaging yields good predictive estimates (ter Braak & van Dam 1989; Oksanen *et al* 1988), reasons why weighted averaging has been used here.

Invertebrate sampling for the years 1989 and 1991 occurred during high rainfall and this is reflected in the canonical analysis by the relatively long arrows for flow, with the close association with rheostenic species. Species composition appears to be relatively unchanged from one year to the next, although there are some marked differences in species abundance. Increasing the number of environmental variables from 11 to 32 for the canonical analysis did not make for a conclusive ordering of sites with regard to these variables and species composition. The large number of variables in the datasets analysed using CANOCO presented problems. There was a high degree of covariance and multicolinearity was detected by the program and, therefore, intraset correlation coefficients were used to overcome this. With the exception of Old Lodge, none of the UKAWMN sites are particularly close to source, this is because sampling stations appear to have been chosen mainly for ease of access.

Spring sampling of the stream benthos poses a number of difficulties. Timing the occasion to collect samples before the dominant insects go on to pupation or emergence is a balancing act; and if early emerging species have already mated and laid eggs, the invertebrates in their first instars are often difficult to identify. There is well documented evidence that temperature differences influence patterns of distribution (Brittain 1982). This may be relevant when dealing with stream systems ranging from the south of England to the North of Scotland. For example, Lillehammer (1975), reported that a local population of *Leuctra hippopus* exhibited a marked divergence in emergence period compared to a stream of similar elevation but having a slightly different thermal regime. These specimens also exhibited a higher degree of short wingedness than other populations of *L. hippopus*. In contrast, statistical analysis from research by Aston *et al* (1985) indicates that there may be a stronger relationship between insect biomass and alkalinity, rather than biomass and temperature.

Acid waters are characterised as often being fishless, with low species diversity and low productivity. Although invertebrate communities in sites of low pH exhibit an overall impoverishment, the relative or absolute abundance may actually increase because of a more rapid decline of certain taxa intolerant of declining pH. Caution needs to be exercised because, in addition to chemical interrelationships (e.g. the relationship between hardness and pH and the indirect effects this may have on species interactions), many other chemical and non-chemical factors may also covary with a parameter such as water hardness. For example, soft waters tend to occur near the headwaters, where summer temperatures are usually lower and oxygen concentrations higher than in the hard waters lower in the catchment. Care is therefore required when drawing conclusions about factors controlling the distribution of aquatic insects, as temperature, altitude or substrate may be partly responsible for the observed faunal patterns.

All stream sites examined here have low pH in common. The indications (from CCA) are that flow and temperature are also consistent variables of importance. We have seen that, while the measures of persistence are high, the patterns from ordination are not concordant from one year to the next, while site 13 (Old Lodge) remains a general outlier. There are obvious differences in physical and chemical variables which separate out these stream sites, although some sites do group together, e.g. sites 2 & 3 and sites 19 & 20. In Chapter 6, the Ashdown Forest and the UKAWMN stream sites are analysed together, and one might expect to see the acid stream sites from the Ashdown Forest falling out, to some degree, with the UKAWMN stream sites.

CHAPTER 6.

COMMUNITY PATTERNS IN THE COMBINED SUITE OF SITES.

6.i. INTRODUCTION.

Taxonomic composition is difficult to assess because communities change through the addition and loss of species. Patterns in community persistence will be very sensitive to the time scale at which it is measured, whether it be the turn-over of one generation or in geological time. A community maybe considered to have 'structure' if the species it contains are a nonrandom subset of the available pool of species available. For instance, further species may be actively excluded because they are unable to colonise for a variety of ecological reasons (Pimm 1991). The indirect approach to community ecology attempts to infer process from these patterns in species composition, an approach which has been highly controversial (Lewin 1983). It is usually assumed that community patterns are stable and repeatable, and this has been discussed in Chapter 1. To equate pattern with persistence, however, requires an assumption that the community has a 'home-field' advantage. That is, where there is competition between the existing species in a community and an invader, 'residents' usually win, with invading species able to enter communities only in a way that maintains some 'community pattern'.

The idea of the community is a central one in ecology. It is a complex notion, however, meaning different things for each major taxonomic or resource-sharing group. As the scope of a study is expanded in time and space (and therefore in heterogeneity), the nature of the community changes radically. A general definition of the term "community" is given by Allen & Hoekstra (1992) as a complex whose parts must be accommodated to each other in some way, otherwise the community is just an arbitrary collection. It is a mistake, however, to assume that everything is connected, most species are not connected to more than a few others (Levins 1974; Margalef 1972; MacArthur 1972; May 1974).

Ecological problems usually involve numerous variables and numerous individuals or samples, which it is now possible to analyse with the use of computers. Community data, are by their very nature, multivariate because numerous environmental factors potentially affect communities. Multivariate analysis is a branch of mathematics which allows the summary of large, complex sets of data, dealing with numerous variables simultaneously. The purpose of the analysis is to treat multivariate data as a whole, summarising the data and revealing their structure. The development of ordination techniques by Curtis (1959) and Whittaker (1956) and of classification techniques by Goodall in the 1950s (1953, 1954) made it possible to group similar species and similar sites together. These multivariate methods have since been extended to include not just species associations but sites and environmental parameters - and used to define 'community boundaries' (Gauch 1982). Although initially used for vegetational analysis (Gauch *et al* 1974; Swaine & Greig-Smith 1980; ter Braak 1987 *b*), they have gained broad acceptance as a useful tool in many other community studies (Dixit *et al* 1991; Rossaro 1991; Stevenson *et al* 1989). One approach to studying patterns in streams, therefore, has been to correlate species distribution with environmental parameters using multivariate techniques. Perhaps the best example of this in Great Britain is the extensive survey undertaken by Wright *et al* (1984) and Furse *et al* (1984), where 268 sites on 41 river systems were sampled over three seasons and classified on the basis of species composition and environmental factors, such as water chemistry, substrate type, channel width and slope. This has developed into such a sucessful predictive tool that the National Rivers Authority now uses the River InVertebrate Prediction And Classificatin System (RIVPACS) in monitoring (Wright *et al* 1989). Previous studies using macroinvertebrate communities implicated pH as a major factor in species distribution patterns and have been remarkably consistent (Sutcliffe & Hildrew 1989). Acidification has been identified in previous chapters as an important variable in structuring some stream communities in the Ashdown Forest suite of sites. The same patterns were not so clear for the UKAWMN.

In this Chapter, both the Ashdown Forest and the United Kingdom Acid Waters Monitoring Network (UKAWMN) stream sites have been treated together to look at overall spatial relationships in species composition and at patterns of persistence. Chapters 4 and 5 looked at each suite of sites independently. The Ashdown Forest stream sites (Chapter 4) with a low pH, low summer temperatures and that are close to the source exhibited a high degree of persistence over thirteen years. In contrast, persistence was seen to be more generally high for the UKAWMN stream sites (Chapter 5), but did not consistently vary with pH. It is, therefore, possible that some other factor, perhaps geographical, dominates these patterns, or there may be an overall upland/lowland difference or some other physical or chemical factor. My main objective in this Chapter is to examine the combined data sets to ascertain what variable(s) most influence these stream communities.

6.ii. METHODS.

Invertebrate sampling.

Twenty-nine stream sites in the Ashdown Forest were sampled in October 1989 and in April 1990 and eleven stream sites from the United Kingdom Acid Waters Network (UKAWMN) were sampled in April/May 1990 and October 1990. (Old Lodge1 from the Ashdown Forest and 'Ashdown Sands' from the UKAWMN is the *same* site). Five Surber samples (area 0.0625 m^2, 330um mesh size) were taken from riffle sections at each site. Substrate was removed to a depth of approximately 5cm and all the material collected was preserved in the field using 4% Formaldehyde. Samples were hand sorted in the laboratory after sieving. Invertebrates were identified to species level using a variety of taxonomic keys. Counts were made and a species by sites matrix was compiled on a spreadsheet.

Environmental variables.

Minimum and maximum temperature (^0C), mean, minimum and maximum pH, conductivity ($\mu S\ cm^{-1}$) and mean discharge ($m^3\ s^{-1}$) were recorded. Chapter 4 gives recording and instrument details for the Ashdown Forest sites and Chapter 5 for the UKAWMN sites.

Statistical analysis.

A matrix of species by site was constructed from the raw data for the spring and autumn samples. Sample units were pooled. As the samples had a negative binomial distribution they were given a $\mathrm{Log}_{10}\ (x+1)$ transformation (Elliott 1977) and the adequacy of the transformation was confirmed by plotting the means before and after the transformation. Bartlett's test was used to test for homogeneity of the variances. Persistence measures and multivariate methods for analysisng data were described in Chapter 4.

6.iii. RESULTS.

6.iv. Physicochemical variables.

Physicochemical variables are presented in Table 6.1 and a matrix of Pearson's product-moment correlation coefficients is presented in Table 6.2. The horizontal line separates UKAWMN (above) and Ashdown Forest sites (below).

TABLE 6.1: Table of physicochemical variables for forty stream sites.

Site	mean pH	pH min	pH max	Temp min	Temp max	Discharge	Cond
ACNC	6.0	5.3	6.5	4.5	9.8	0.78	23.6
AAM	4.1	5.1	6.8	2.6	6.2	0.49	39.0
DL	5.3	5.0	6.9	4.0	12.5	0.47	34.1
GB	5.6	4.6	6.9	4.1	10.9	0.45	35.1
RE	4.8	3.8	6.0	2.0	12.0	0.71	82.3
AS	4.4	4.1	4.7	5.7	14.7	0.06	95.5
NB	5.6	5.2	6.2	6.4	11.5	0.42	47.8
BB	5.2	4.6	7.2	4.1	12.5	0.34	57.5
BR	5.2	4.4	6.1	4.7	18.0	0.42	44.3
CG	6.3	5.7	7.0	2.1	9.9	0.35	56.6
AH	5.4	4.8	5.3	4.4	9.5	0.61	38.6
LB	5.7	4.6	6.7	1.0	8.0	0.35	40.3
LP	6.4	5.6	7.0	3.4	13.9	0.04	125
WR	6.7	6.5	6.8	2.4	17.1	0.06	202
KBP1	5.9	5.6	6.4	2.0	15.3	0.06	153
KBP2	5.5	5.2	5.8	1.5	14.4	0.06	222
NB	6.2	5.4	6.7	3.0	15.0	0.08	211
OL	4.6	4.2	4.9	3.6	15.5	0.05	98
CH	5.0	4.7	6.2	4.1	14.6	0.08	112
LO	4.8	4.4	5.3	4.0	15.0	0.06	105
CW	6.7	6.3	7.2	4.0	16.0	0.04	216
NU	6.8	6.5	7.3	3.7	16.3	0.03	229
CS	6.6	6.2	6.8	4.0	14.7	0.13	230
DB	6.4	6.0	6.7	4.0	16.1	0.08	130
OLS	6.8	6.3	6.9	4.1	16.7	0.11	158
FW	5.9	5.4	6.7	3.8	16.0	0.20	188
MH1	6.8	6.4	7.2	4.0	15.9	0.24	176
MH2	6.4	6.0	6.7	4.0	16.0	0.26	181
BFG	6.5	6.3	6.8	3.8	16.1	0.20	187
OF	6.7	6.2	7.2	3.4	16.7	0.18	197
BBG	7.0	6.7	7.2	3.5	17.0	0.40	225
HL	6.7	6.5	6.9	4.0	16.4	0.25	171
MF	6.5	6.3	7.0	3.8	16.6	0.30	198
MG	6.6	6.4	6.8	3.6	16.8	0.43	134
PB	6.6	6.4	6.91	3.6	16.7	0.36	168
HMI	6.5	6.3	7.0	4.0	16.6	0.39	235
WY	6.8	6.6	7.2	4.0	16.8	0.44	227
WH	6.9	6.5	7.1	4.1	16.7	0.41	273
BWM	6.8	6.5	7.1	4.1	17.3	0.13	199
BS	5.3	4.8	6.0	2.1	15.4	0.06	86

Table 6.2: Matrix of Pearson correlation coefficients between physicochemical variables measured at forty stream sites. Correlations significantly different from zero, p* <0.01,(critical value of $r = 0.358$).

	Mean pH	Min. pH	Summer Temp	Discharge	Conductivity
Mean pH	1	0.91*	0.40*	-0.18	0.67*
Min. pH		1	0.63*	-0.35	0.78*
Summer Temp.			1	-0.51*	0.75*
Discharge				1	-0.46*
Conductivity					1

6.v. Persistence

Community persistence, measured by Spearman's rank correlation coefficients of the relative abundance of species for spring and autumn samples 1990 (for UKAWMN sites) and autumn 1989 and spring 1990 (for Ashdown Forest sites) are plotted against pH, summer temperature and conductivity in Fig 6.1 a, b & c. Points which occur over to the left hand side of the graphs generally have significant correlation coefficients of 0.5 and above, indicating that streams with low pH, low summer temperatures and low conductivity tend to be more persistent. In Fig 6.2, other measures of persistence are plotted against pH, summer temperature and conductivity for forty stream sites. Here, Sorenson's index of similarity is used and again there is a marked trend for the sites over to the left hand side of the graph (with low pH, low summer temperatures and low conductivity) to have greater persistence. Table 6.3 gives Spearman's r and Similarity indices for 40 sites, twelve UKAWMN sites and 28 Ashdown sites. Old Lodge 1 (OL1) is given as AS in the UKAWMN list.

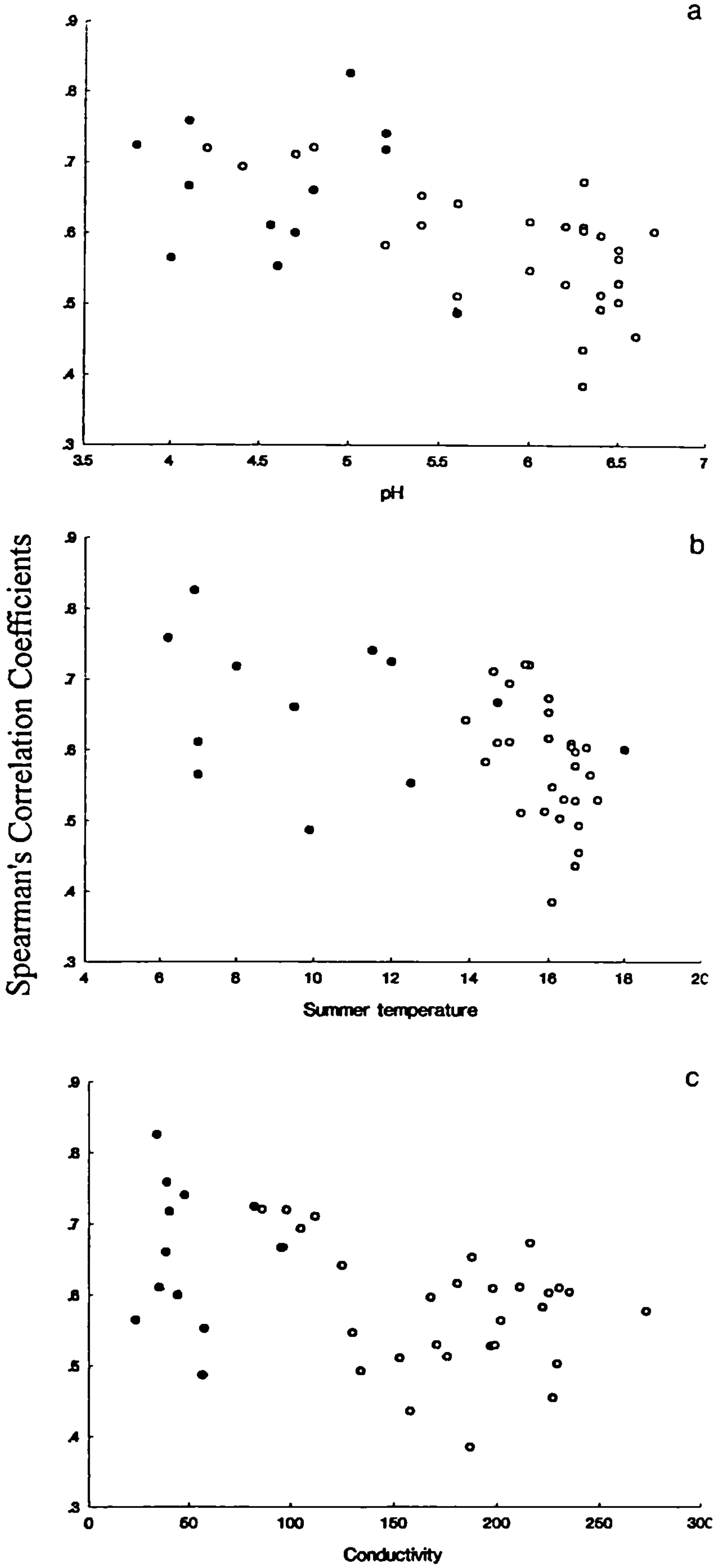


Fig. 6.1: Persistence in rank abundance of species (Spearman's correlation coefficients) for the total community (1989-90), plotted against pH (a), summer temperature (b) and conductivity (c). A Spearman's *r* greater than 0.5 is a significant positive correlation. Stream sites with low pH, low summer temperatures and low conductivity generally have high correlation coefficients. UKAWMN sites are in red and Ashdown Forest sites are uncoloured. Old Lodge, which is included in both suites of sites, is in blue.

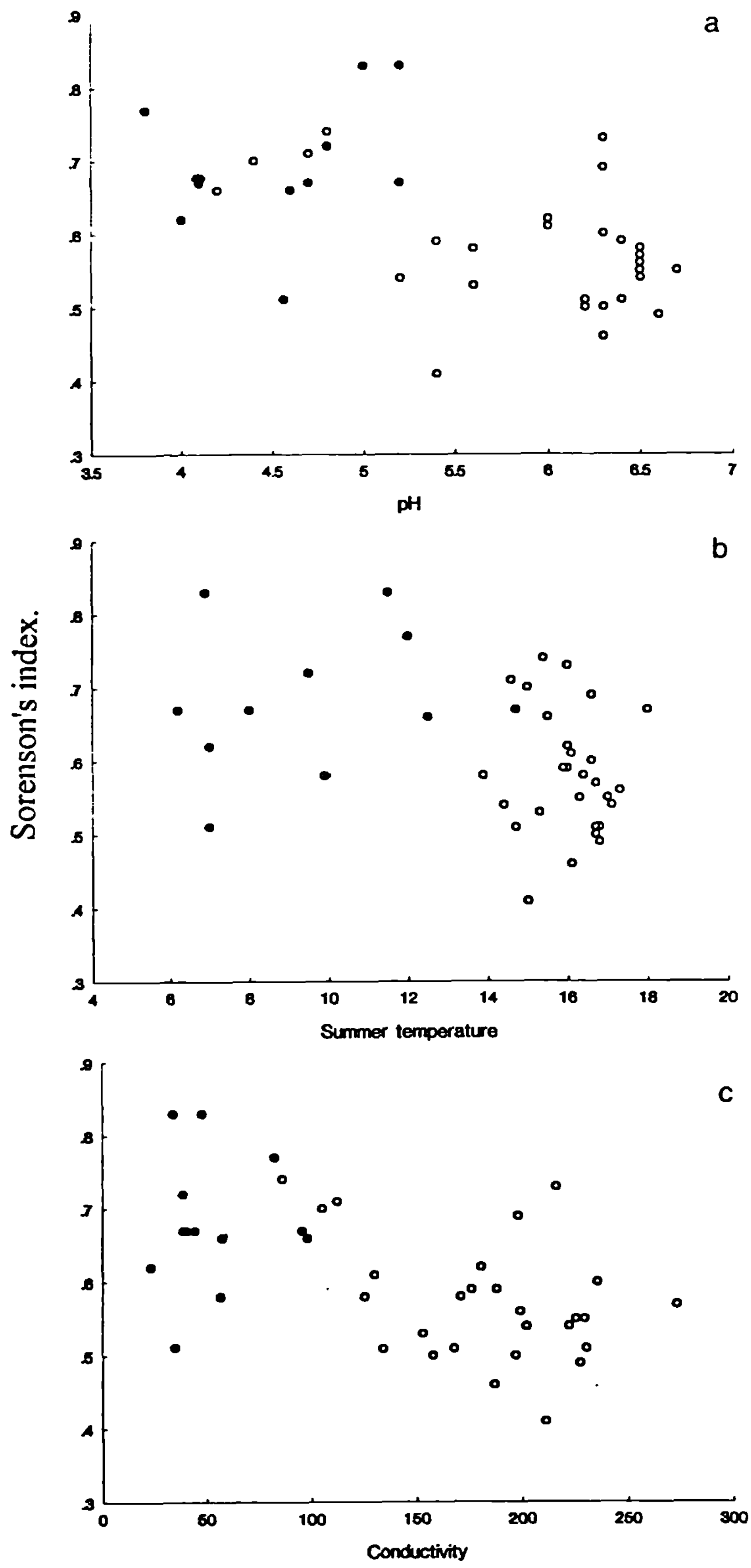


Fig. 6.2: Persistence in community composition (measured as Sorenson's index) is plotted against pH (a), summer temperature (b) and conductivity (c). Sorenson's index of similarity ranges from 0-1, from no similarity to complete similarity. An index of over 0.5 is significant and a pattern of high similarity can be seen for stream sites with low pH, low summer temperature and low conductivity. UKAWMN sites are in red, Ashdown Forest sites are uncoloured. Old Lodge, which is included in both suites of sites is in blue.

Table 6.3 Measures of persistence in rank abundances (Spearman's *r*) and species composition (Sorensons and Jaccard's indices) for 40 sites.

SITE	Spearman's *r*	Sorenson's index	Jaccard's index.
UKAWMN			
ACNC	0.56	0.62	0.59
AAM	0.75	0.67	0.60
DL	0.82	0.83	0.74
GB	0.61	0.51	0.49
RE	0.72	0.77	0.65
AS	0.66	0.67	0.61
NB	0.74	0.83	0.74
AH	0.72	0.61	0.55
LB	0.79	0.63	0.62
BB	0.55	0.67	0.64
BR	0.56	0.54	0.49
CG	0.45	0.46	0.33
ASHDOWN			
LP	0.57	0.58	0.43
WR	0.51	0.53	0.47
KBP1	0.51	0.53	0.50
KBP2	0.58	0.54	0.51
NB	0.61	0.41	0.39
OL	0.72	0.66	0.63
CH	0.71	0.71	0.68
LO	0.69	0.70	0.66
CW	0.67	0.73	0.65
NU	0.50	0.55	0.46
CS	0.61	0.51	0.48
DB	0.54	0.61	0.55
OLS	0.43	0.50	0.43
FW	0.65	0.59	0.51
MH1	0.65	0.59	0.49
MH2	0.61	0.62	0.56
BFG	0.38	0.46	0.41
OF	0.52	0.50	0.47
BBG	0.60	0.55	0.48
HL	0.53	0.58	0.52
MF	0.60	0.69	0.61
MG	0.49	0.51	0.45
PB	0.59	0.51	0.46
HMI	0.60	0.60	0.57
WY	0.45	0.49	0.44
WH	0.57	0.57	0.49
BWM	0.52	0.56	0.51
BS	0.72	0.74	0.66

6.vi. Spatial relationships.

The TWINSPAN site classification results for the autumn Surber samples are given in Fig 6.3. The dendrogram illustrating the results is taken only to the second level. The first positive division gives a separation related to pH, with all the UKAWMN sites (initials in capital letters) and the low pH sites from the Ashdown Forest (lower case initials) separating out together, while the circumneutral Ashdown Forest sites fall into the first negative division. The 'indicator' species listed include *Siphonoperla torrentium* and *Leuctra nigra* for the first positive division and *Baetis spp* for the first negative separation. In the second division the UKAWMN sites separate from the Ashdown Forest sites. Both summer temperatures and mean annual discharge appear to be implicated and it has not been possible to say which plays the major role. Again, acid tolerant species such as *Plectrocnemia geniculata, P. conspersa* and *Niphargus aquilex,* appear as 'indicator' species for the divisions off from the first positive division and *Sericostoma personatum* for the separation off from the first negative division. The only sites to separate further (not shown here) are Alt a' Mharcaidh (AAM) and Alt Coire nan Con (ACNC) from the left hand side and Old Lands (OLS) from the right, and no environmental factor presents itself as being responsible. The capital letters 1 2 3 & 4 relate to the DEtrended CORrespondence ANAlysis below.

Fig 6.4 gives the DECORANA plot for autumn samples and four groupings have been identified. These, in turn, relate to the TWINSPAN dendrogram above. The first axis is positively correlated with pH and the second negatively with summer temperature.
In Fig 6.5: the TWINSPAN groupings for spring are depicted in a dendogram. The sites separate out as for the autumn classification at the first division but, for the second division, Nutley (nu) moves from final group 3 across to 2. Pooh's Bridge (pb), Fairwarp (fw), Batt's Bridge (bbg), Marsh Green (mg), Maresfield (mf) all move from final group 3 to 4 and Half Moon Inn (hmi) moves from 4 to 3. Interestingly, these are mainly circumneutral stream sites. Indicator species are similar and the first division relates to pH and the second to temperature.

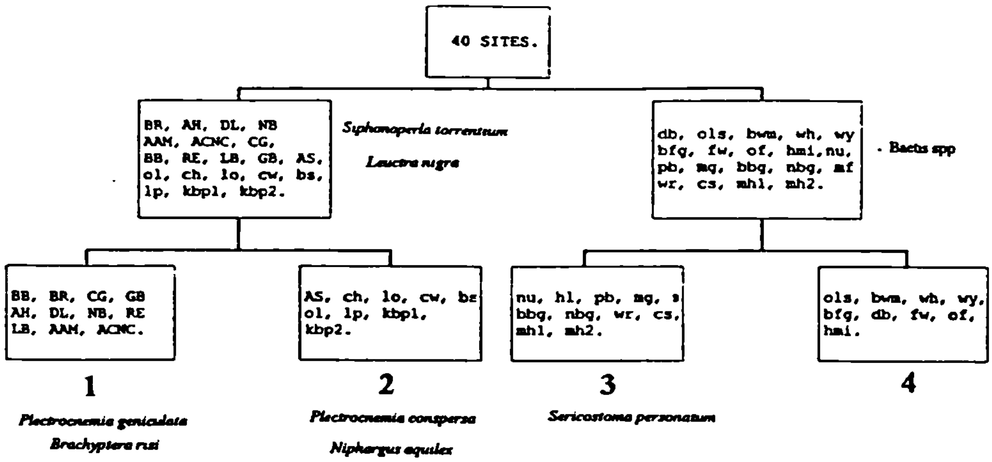


Fig. 6.3: TWINSPAN dendogram for the autumn Surber samples. Forty sites taken to two divisions only. The numbers (1 2 3 & 4) relate to the detrended correspondence analysis below. The first division gives a separation of sites on pH and the second division on mean annual temperature. Indicator species are given with each division. Capital letters denote the UKAWMN sites.

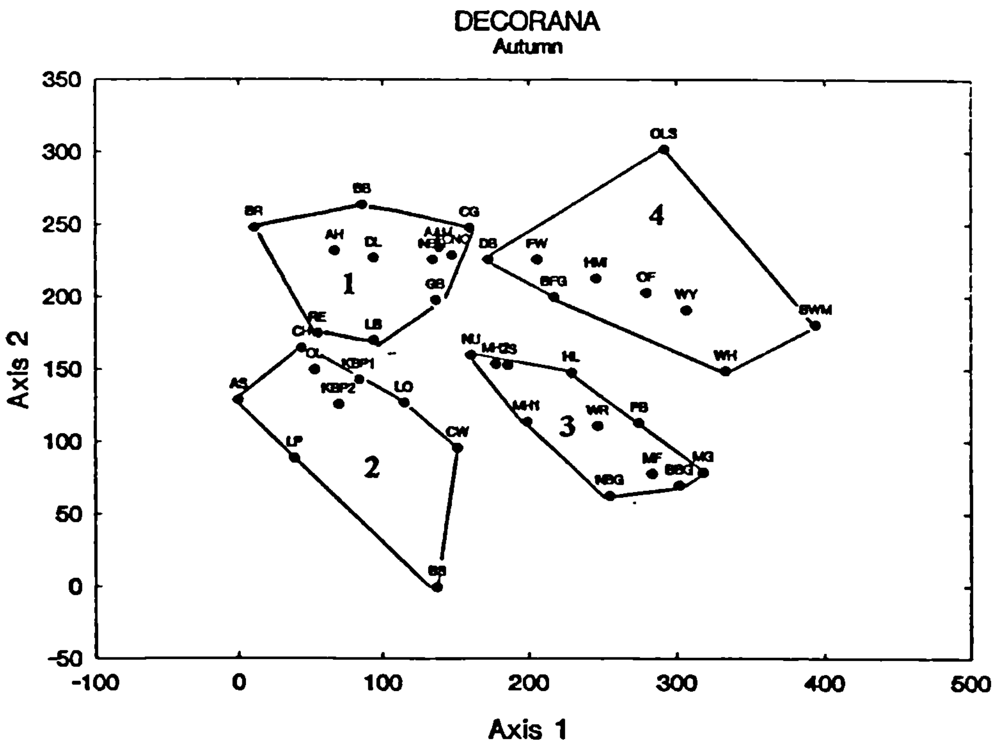


Fig. 6.4: DECORANA plot for autumn. Four groupings have been identified which relate to the TWINSPAN groupings. The first axis is positively correlated with pH and the second axis with temperaure. UKAWMN sites are bounded by red polygons.

Table 6.4 gives the Eigenvalues, percentage and cumulative percentage variance explained and lengths (in standard deviations) of DECORANA axes for autumn and spring, and the plot for the spring 1990 DECORANA is given in Fig 6.6. Again, four groupings have been identified and indicated by a number, which corresponds to the TWINSPAN groupings. The first axis is positively related to pH and the second negatively related to temperature.

Table 6.4: Eigenvalues, percentages and cumulative percentage variance explained and lengths (in standard deviations) for DECORANA axes for autumn and spring samples.

Autumn

	Eigenvalue	% var explained	cum % explained	length (SD)
Axis 1	0.400	44.8	44.8	2.11
Axis 2	0.293	30.2	75.0	1.56
Axis 3	0.201	19.2	94.2	1.33
Axis 4	0.098	5.8	100.0	1.47

Spring

	Eigenvalue	% var explained	cum % explained	length (SD)
Axis 1	0.525	54.6	54.6	1.91
Axis 2	0.294	35.2	89.8	1.63
Axis 3	0.231	8.3	98.1	1.27
Axis 4	0.092	1.9	100.0	1.47

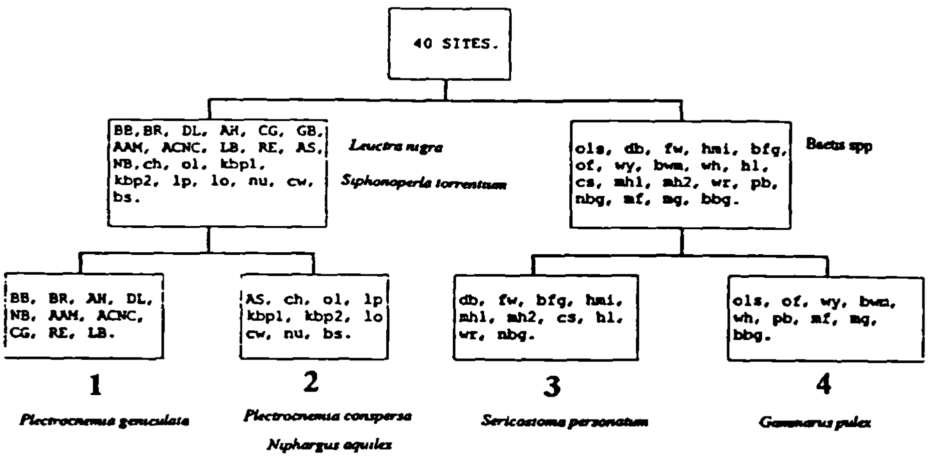


Fig. 6.5: TWINSPAN groupings for spring. The numbers 1 2 3 & 4 relate to the detrended correspondence analysis below. Indicator species are given at each division, and capital letters denote the UKAWMN sites and lower case letters the Ashdown Forest sites. The first division relates to pH and the second to temperature.

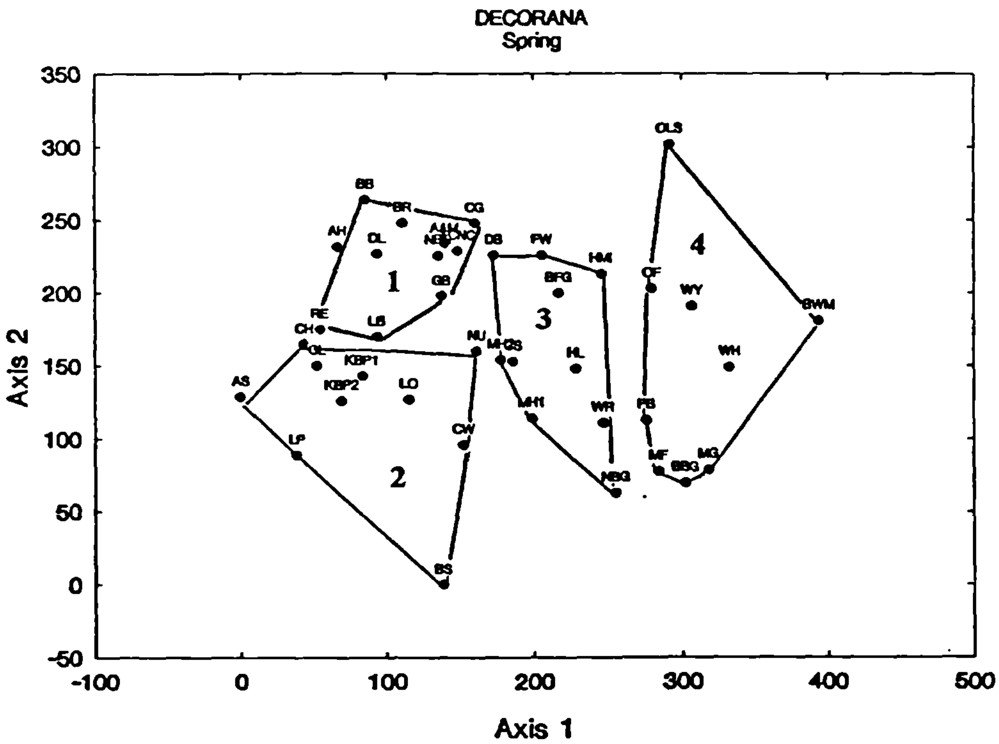


Fig. 6.6: DECORANA plot for spring 1990. Four groupings have been identified which relate to the TWINSPAN divisions given in Fig. 6.5. The first axis is positively related to pH and the second to temperature. The UKAWMN sites are surrounded by a red polygon.

For the autumn samples the first two axes explain 75% of the variation and for the spring samples the first two axes account for 89.8% of the variation. Table 6.5 gives the results of the product-moment correlation coefficients between the physicochemical variables and scores for the DECORANA axes 1, 2 & 3 for the autumn and spring samples.

Table 6.5: Product-moment correlation coefficients between site scores on DECORANA axes 1,2 & 3 and environmental variables.

Autumn.

	AXIS 1	AXIS 2	AXIS 3
Mean pH	0.805***	-0.098	-0.102
Minimum pH	0.770***	-0.207	-0.109
Temperature	0.443*	-0.371*	0.087
Discharge	-0.017	0.337*	0.157
Conductivity	0.637**	-0.383	-0.038

Spring

	AXIS 1	AXIS 2	AXIS 3
Mean pH	0.799***	-0.110	-0.102
Minimum pH	0.769***	-0.217	-0.109
Temperature	0.486*	-0.383*	0.087
Discharge	0.002	0.337	0.157
Conductivity	0.622**	-0.371*	-0.038

In Table 6.6 the multidiscriminant analysis predicting the TWINSPAN groupings using the environmental variables is given for spring data.

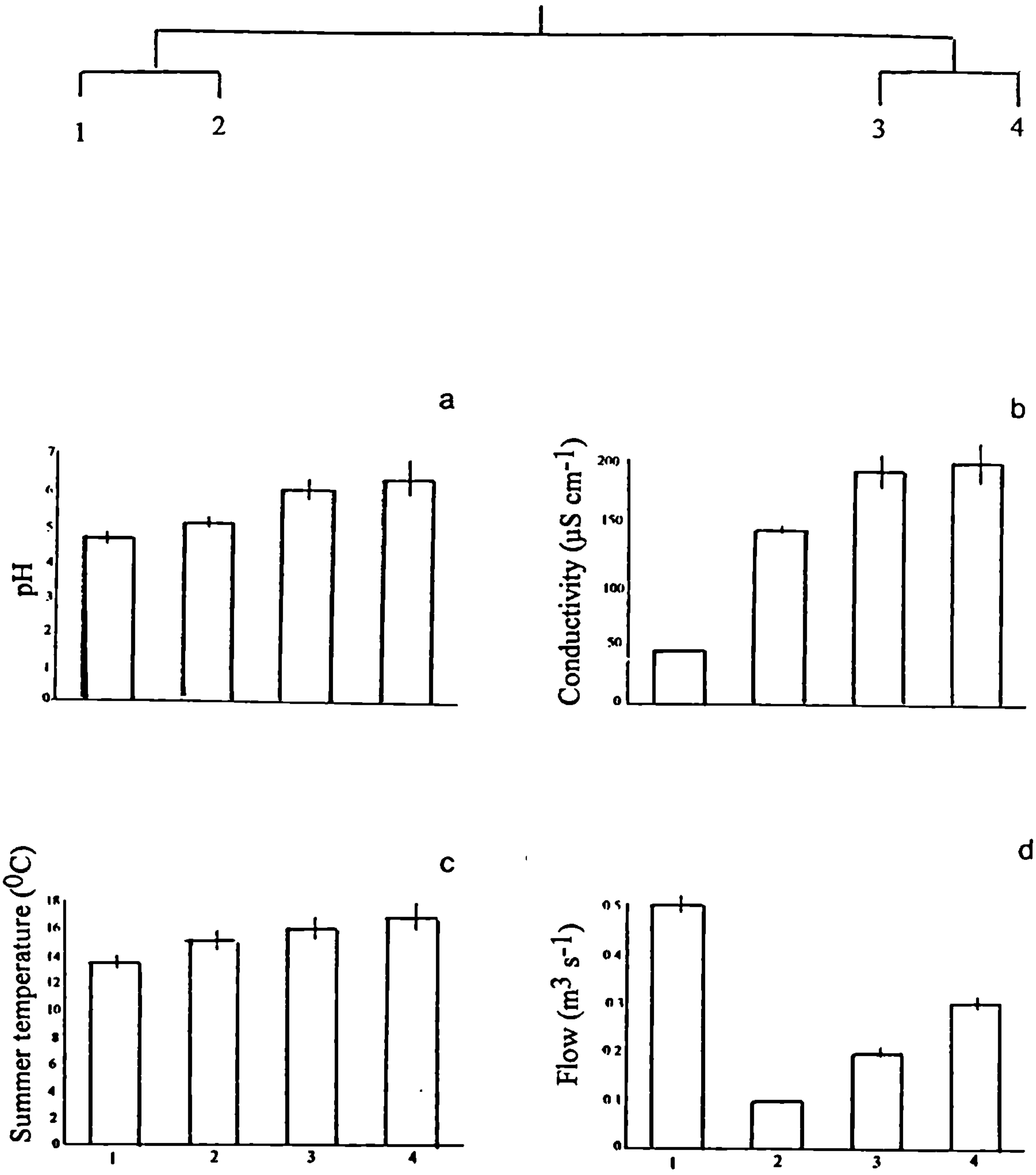


Fig. 6.7: The TWINSPAN groupings for spring 1990 are featured at the top of the figure as 1 2 3 & 4. Mean values from environmental variables of sites falling into each group are given. Numbers at the bottom of each plot corresponds to the TWINSPAN groupings. The environmental variables are, pH (a), conductivity (b), summer temperature (c) and flow (d). Sites in group 1 are those with pH below 4.7, conductivity below 50 µS cm^{-1} , summer temperatures below 14 ^{0}C and flow (mean discharge) above 0.50 (m^3 s^{-1}).

Table 6.6: The percentage of sites predicted to the correct TWINSPAN grouping using multiple discriminant analysis (Spring data).

	TWINSPAN LEVEL	
	1	2
Number of significant discriminant functions ($P< 0.05$).	2	4
% of correct predictions.	77.8	74.6
% of sites in which correct group is the second most probable.	22.2	25.3

TWINSPAN groupings for the spring samples are given in Fig 6.7. The groupings are featured at the top of the figure as the numbers 1 2 3 & 4. The main values for four environmental variables at the forty sites (pH, summer temperature, conductivity and maximum discharge), and divided into the four groupings, are also shown. The first three variables show an increase in the mean values across the groupings 1-4. For flow (discharge), however, there is a high mean value for group 1 (the UKAWMN sites except for Ashdown Sands), then a drop in group 2 and a modest increase through to group 4. The maximum discharge for the UKAWMN sites, bar Ashdown Sands (Old Lodge), was significantly larger than for the Ashdown Forest stream sites.

Canonical analysis was carried out for all sites for both autumn and spring 1990. Fig 6.8 gives a canoplot for the forty sites in autumn. The black dots are species although, to avoid obscuring the picture, only a few species are actually named. Sites are represented by capital initials and environmental variables by black arrows. The length of the arrow is an indicator of the strength of an association and here pH has the longest arrow. The first axis is strongly correlated with pH in particular, but also with flow, and the second axis with temperature. In Fig 6.9 the species are plotted in conjunction with a major environmental variable, in this case pH. Perpendicular lines are drawn from the labelled species to the arrow. The intersecting points identify approximate weighted mean values of the specific environmental variable and each taxon. As can be seen from this canoplot, acid tolerant species such as *Plecrocnemia conspersa* lie closest to the arrow.

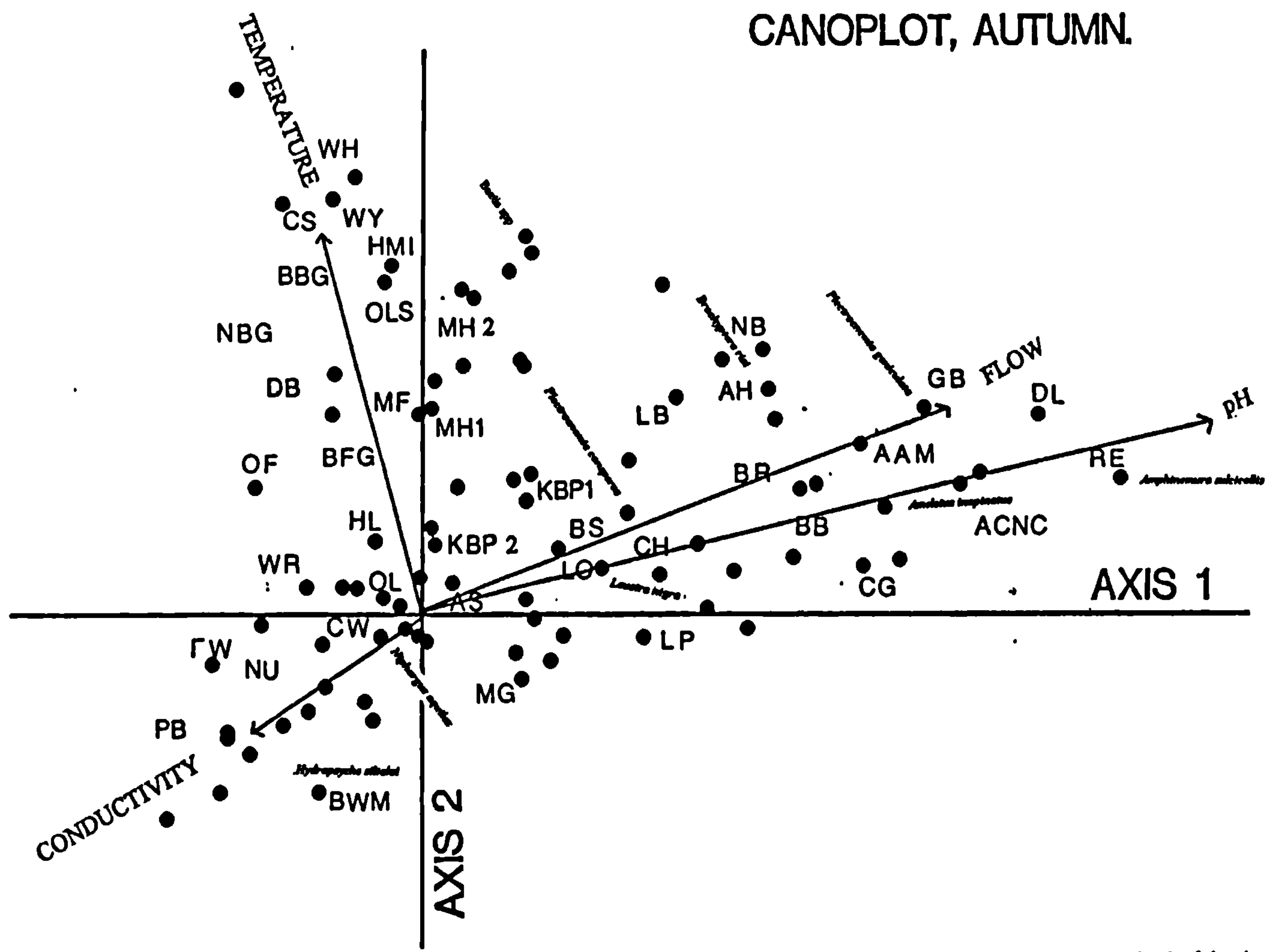


Fig. 6.8: CANOPLOT for the autumn samples. The first axis is strongly correlated with pH and flow and the second axis with temperature. Each of the sites is plotted with the initials in capital letters, and each species is depicted by a black dot, only a few of which are named. The environmental variables are shown as black arrows and the length of the arrow is an indicator of the strength of the association.

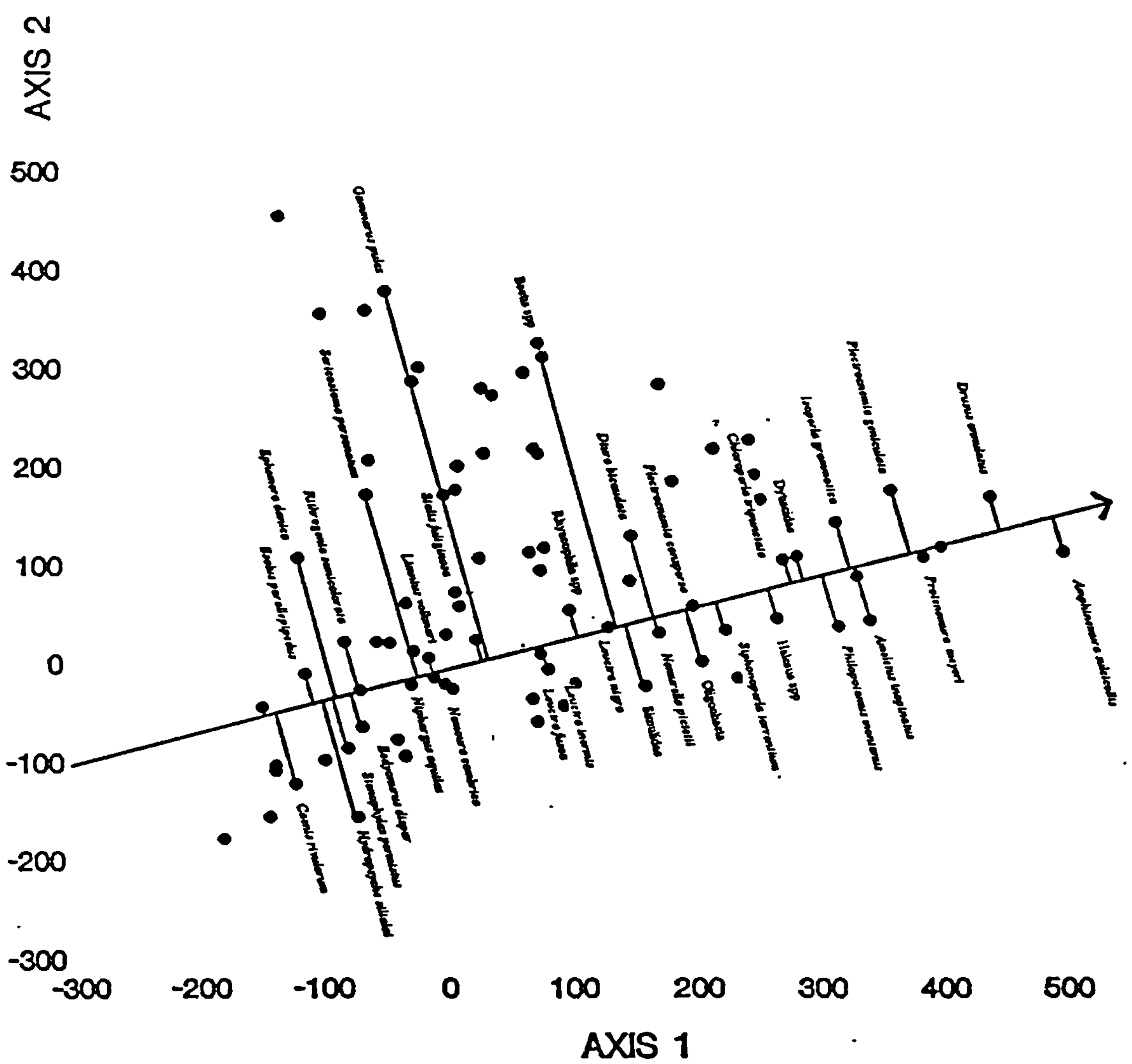


Fig. 6.9: CANOPLOT for autumn samples with species and one major environmental variable (pH). Perpendicular lines are drawn from the species to the arrow. The intersecting points identified approximate weighted mean values of the specific environmental variable for each taxon. Species closest to the arrow include *Plectrocnemia conspersa*, *Niphargus aquilex*, *Leuctra nigra* and nemourid stoneflies - acid tolerant taxa as would be expected.

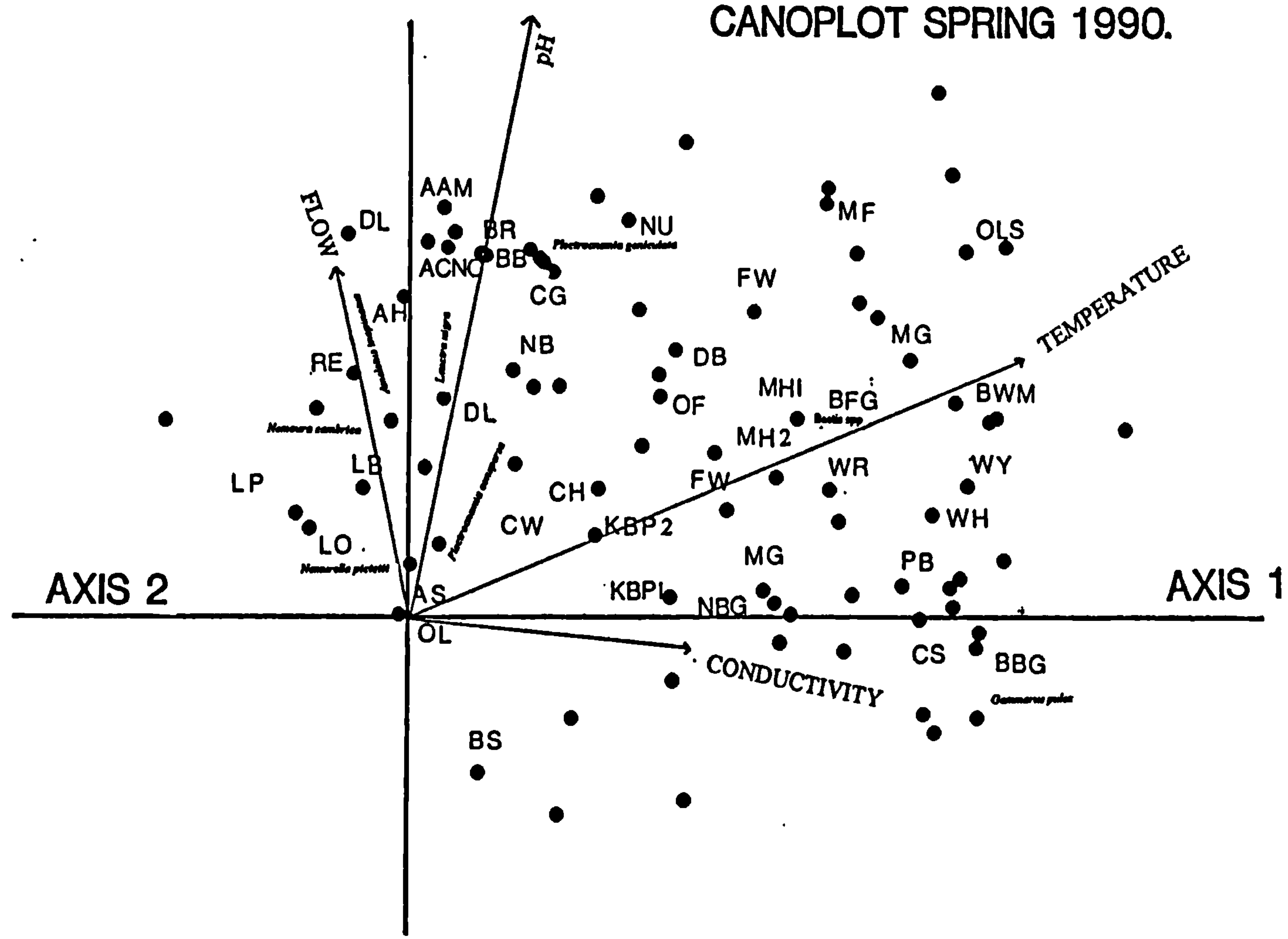


Fig. 6.10: CANOPLOT for spring 1990. The first axis is correlated with temperature and conductivity and the second axis with pH and flow. Each species is depicted as a black dot, only a few are named. Sites are given as initials in capital letters and environmental variables as black arrows. The length of the arrow is an indicator of the strength of association, and here the longest arrow is for pH.

The spring samples analysed using CANOCO are represented in the canoplot in Fig 6.10. Here the first axis is correlated with temperature and conductivity and the second axis with pH and flow. The longest arrow is that for temperature. Sites are given as capital initials and only a few species are labelled. Fig 6.11 is a canoplot for the spring samples with pH as the major environmental variable given as an arrow. The arrow points in the direction of maximum change of that variable across the diagram, and its length is proportional to the rate of change in this direction. Again the arrow is extended in the opposite direction and perpendicular lines are drawn from the species to the arrow. it can been seen that acid tolerant species, such as *Nemurella picteti* and *Niphargus aquilex*, lie closest to the arrow. Table 6.7 gives the correlation matrix showing the relationship between axes and environmental variables.

Table 6.7: Correlation matrix showing the relationship between axes and environmental variables for autumn and spring samples.

Autumn				
	Axis 1	Axis 2	Axis 3	Axis 4
Mean pH	0.523	-0.210	-0.233	0.009
Min pH	0.597*	0.127	0.115	-0.124
Temperature	0.444	0.416*	-0.202	-0.115
Flow	0.421	0.158	-0.171	-0.098
Conductivity	-0.041	0.171	-0.201	-0.056

Spring				
	Axis 1	Axis 2	Axis 3	Axis 4
Mean pH	0.424	0.226	0.187	0.204
Minimum pH	0.514	0.621*	0.235	0.106
Temperature	0.640*	0.537	0.334	0.257
Flow	0.225	0.312	-0.252	-0.064
Conductivity	0.352	0.171	-0.322	-0.225

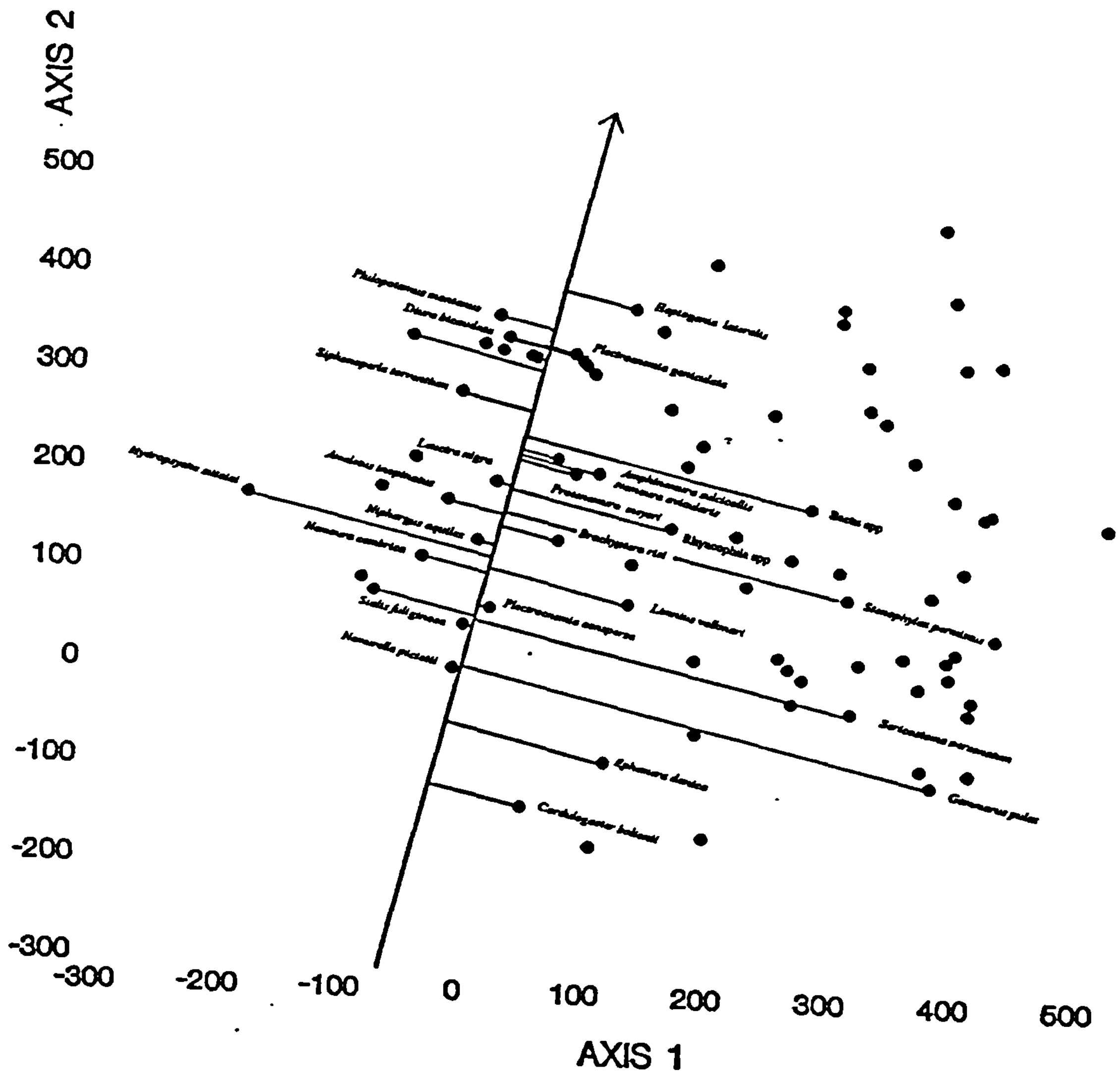


Fig. 6.11: CANOPLOT for spring 1990 with species and one major environmental variable (pH). Perpendicular lines drawn from the species to the arrow. The intersecting points identifies approximate weighted mean values of the specific environmental variable and each taxa. Species closest to the arrow are those tolerant of acid conditions.

6.vi. DISCUSSION.

Consideration of the whole suite of sites, from both the Acid Waters Monitoring Network and the Ashdown Forest, gives some indication that the persistence of macroinvertebrate communities is related to pH or correlated variables. Sorenson's and Jaccard's similarity indices measured similarity in species composition between autumn and spring. All UKAWMN sites had a Sorenson's index greater than 0.5, as did the low pH sites from the Ashdown Forest. Species at UKAWMN sites also had had a breeding season between sampling occasions. Samples from the Ashdown Forest streams were not separated by a breeding season, however. This is because these samples were the only data available that covered more than one season (previous years samples were taken in the autumn). We have data taken over at least one breeding season and the results are very similar, the acid streams had high persistence measures and the circumneutral streams were more variable. Seasonal data from the UKAWMN showed these sites to behave in this analysis as they did in the between-year analyses. There was a general trend whereby those sites with the highest persistence measures had low pH, low summer temperatures and low conductivity. The Spearman's rank correlation coefficients for the total community were also significant. That is to say, there was a good correlation between the autumn and spring samples. Again, we saw that there was a general trend for the sites with the highest Spearman's *r* to have low pH, low summer temperatures and low conductivity.

With regard to the multivariate analysis, here the patterns were consistent for the two sampling occasions. The TWINSPAN groupings separated out on pH and temperature. Ashdown Sands, or Old Lodge (site 7), from the Ashdown Forest suite of sites, moved away from the UKAWMN sites at the second division. These patterns were evident in the plots for DECORANA for both autumn and spring. Unfortunately, the number of environmental variables available for analysis was restricted. Although the

UKAWMN sites have many physicochemical measurements, there were fewer taken for the Ashdown Forest stream sites and not all of those were comparable. The main environmental parameters used, minimum, maximum and mean pH, minimum and maximum annual temperature, mean annual discharge and mean annual conductivity appear to account for a large percentage of the variability explained by the first two axes in the DECORANA and canonical analysis. Mean values of four environmental variables differed clearly among the four site groupings. Sites grouped in 1, for example, had a mean pH of 4.7, conductivity of 45.4 uS cm^{-1} and summer temperature of 13.5^{0}C. In contrast, group 4 had a mean pH of 6.4, conductivity of 197.7 and summer temperature of 16.8. Discharge was high, (0.49 m^3 s^{-1}) for the UKAWMN sites in group A, while discharge was lowest for sites in group 2 and increased to 0.31 for group 3.

Direct gradient analyses like Canonical Correspondence Analysis (CCA), are valuable in that they allow the probability of occurrence of populations along an environmental gradient to be inferred. Most methods currently available allow for the analysis of only one species at a time (ter Braak 1986). Using CCA it is possible to visualise species distribution along an environmental axis (ter Braak & Looman 1986). Although fewer environmental variables were used than in the analysis of the UKAWMN sites (Chapter 5), there appears to be less ambiguity. The correlations between environmental variables and the axes are significant and it may be the case that the larger number of parameters used in Chapter 5 confused the issue, in that some environmental variables may be correlated with one another (i.e. they covary). CANOCO overcomes this in detecting if multicolinearity occurs, and allowing the intraset correlation coefficients to be plotted. This occurred for the UKAWMN data (Chapter 5) and the intraset correlation coefficients were used. For this dataset, there were no problems with covariance and the subsequent picture was very clear.

The samples used for the analysis were Surber samples, not the kick samples which were taken on the same occasion. Although this should not affect the outcome, as we saw in Chapter 3, I would suggest that using a quantitative sample provides the best 'measure' for the analysis. There were seasonal differences although these were not marked, and the same general pattern occurred.

Surprisingly, the grouping of the two suites of stream sites, the UKAWMN sites and the Ashdown Forest streams, provided a consistent seasonal pattern and confirmed pH as one of the most influential environmental variables. Temperature, discharge and conductivity were also important factors. Ashdown Forest stream sites with low pH, low summer temperatures and low conductivity were spatially aligned with the UKAWMN stream sites, with the Ashdown Forest circumneutral streams separating away from them. The major difference between the acid Ashdown sites and the UKAWMN streams appears to be discharge, with the UKAWMN sites having significantly higher maximum annual discharge. Thus, we can conclude that the ecological similarity between acidic streams throughout Britain is closer than that between chemically dissimilar streams which are in very much closer proximity and, in some cases, within the same river system. This more than anything, demonstrates the powerful effects of 'acidity' (itself a complex of biotic and chemical factors) on stream ecology.

CHAPTER 7.

GENERAL DISCUSSION.

Previous studies of the Ashdown Forest stream sites gave a strong indication that persistence differed among streams. Persistent benthic communities tended to be found in streams close to the source, with low pH and low summer temperatures (Townsend *et al* 1987). Using DECORANA and TWINSPAN to investigate macroinvertebrate community structure, Townsend *et al* found pH to correlate strongly with DECORANA axis 1 and also to relate to the classification groupings. July temperature was the strongest correlate on axis 2 in the 1976 survey but, in 1986, distance from source was the best correlate with axis 2. Having carried out a similar survey of these streams in 1989 and obtained similar results, my data corroborates past surveys and indicates that these results are not an artifact, but good evidence that pH plays an important role in structuring these communities. The acid stream sites, in particular, have remained remarkably 'stable' over the thirteen years since the first survey in 1976 (Townsend *et al* 1983) and there was seen to be a clear separation from circumneutral streams in the classification and ordination of sites. There are exceptions. For example, Boringwheel Mill (site 34) and Lavender Platt (site 1) have experienced changes in surrounding land use and a corresponding increase in pH over the intervening years.

The inclusion of a suite of sites (in the UKAWMN) susceptible to acidification, though not necessarily acid, was an opportunity to look for similar patterns in the benthic invertebrate communities in streams of very different geology, and physical nature from different locations. Using a variety of multivariate analysis, including canonical analysis (using the program CANOCO), I examined the UKAWMN site data for similar patterns of community persistence over a period of four years. The most comprehensive survey of this type, to date, was by Wright *et al* (1984). They surveyed the macroinvertebrates of some 268 sites from 41 rivers in Great Britain, using similar methods. A large number of environmental variables (28) were related to the ordination and classification. In this study, DECORANA axis 1 was correlated strongly with alkalinity and substratum type, and axis 2 with discharge and distance from source. They postulated that the first axis distinguished between different types of river and axis 2 represented a change in communities along a length of a river. In a second analysis of this dataset (Furse *et al* 1984), multivariate methods were employed to make predictions and to catagorize the results. Expanding on this work, these results have been put to good practical use, as National Rivers Authorities now use the classification system RIVPACS to make predictions about the rivers they survey.

Whilst the Ashdown Forest data confirmed earlier evidence of community persistence in acid streams, the UKAWMN data, initially, were not as clear. Persistence measures were generally high, although one site (Old Lodge/Ashdown Sands) had low persistence except for the years 1990-91. The most likely reason for this 'bad fit' may well be the differences in discharge and channel morphology between this site and the rest of the monitoring network. Another explanation could be due to sampling method. However, there were negligible differences between the two sampling methods (Surbers and kicks) for both abundance and numbers of species collected. This stream is also part of the Ashdown suite of sites and, in the Ashdown data set, was amongst the stream sites with the highest persistence measures. It may be that the anomalous behaviour of this site in the UKAWMN was due to a sampling freak. Its benthic community has remained essentially unchanged over the longer period of time it has been studied in the Ashdown Forest project. For the UKAWMN sites the multivariate analysis indicated that there were a number of variables such as flow and temperature that appeared to have a greater significance than pH, although pH was often one of the major correlates on DECORANA axis 2 and in Canonical Correspondence Analysis(CCA) axis 2. The use of a larger number of environmental variables caused problems in that some variables did covary. This tended to obscure the picture, even though CANOCO allows for the intraset correlation coefficients to be plotted, there was obvious covariance e.g. conductivity and [Ca].

When the two suites of sites were combined, there was a clearer separation of stream sites, as was seen in Chapter 6. Spring and autumn Surber samples were used for the combined dataset and only those environmental variables common to both suites of sites were used. Here, there was a consistent pattern, similar for both seasons. Initially, sites separated out on pH, with the UKAWMN and most of the acid Ashdown Forest streams grouped together. At the second division the UKAWMN sites and Ashdown Forest sites separated out on temperature, (Old Lodge/Ashdown Sands with the Ashdown Forest streams). pH was seen to be the variable of greatest association using CCA, with temperature and flow following closely. Discharge would appear to have a large influence on the some of the UKAWMN stream sites. Streams with high mean monthly discharge were Alt Coire nan Con, Alt a' Mharcaidh and Afon Hafren. All three of these streams have wide channels with peak flows occurring in the spring and autumn. These sites often separated out together as was seen in the TWINSPAN classification in Chapter 5. In a comparatively new area of research looking at in-stream flow, Lancaster & Hildrew (1993) identified areas within a stream reach experiencing different degrees of hydraulic stress. It is thought that areas of low flow (which can be detected during flood events) or 'dead zones', may provide refugia for macroinvertebrates during these events. They speculate that the community and its persistence could be determined by the provision of refugia from high shear stress during peak flows. Whether or not other processes, such as the presence of species capable of resisting high flow conditions, are associated with streams of year round high flow rates has yet to be determined.

We have seen that the acid streams within the Ashdown Forest and UKAWMN suites of sites exhibit some evidence of community persistence.Their communities remain, measured in terms of their taxonomic composition and the relative and absolute abundances of species, substantially unaltered over periods of time during which they have experienced some measure of disturbance. Absolute abundance of invertebrates between years may not always tally, but rank abundances of the component species, classification and ordination usually do. It may be that the degree of environmental variation is an important feature in structuring these communities.

Acidification impacts the structure of freshwater communities by the removal of fish and the decline in the diversity of invertebrates (Sutcliffe & Carrick 1973). We also know that the diversity of meiofauna is reduced (Rundle 1988). Persistent, acid sites have cool summer temperatures, and lie upstream and also have the least altered and most retentive channels. It is possible that community persistence relates to the flow refugia provided for in these streams (Hildrew *et al* 1991). Although it has been argued that variable flow regimes and fluctuations in rainfall are likely to reduce community persistence (Meffe & Minckley 1987; Wallace *et al* 1988; Weatherly & Ormerod 1990), some of the sites that I studied experience both of these (UKAWMN sites), in addition to other forms of disturbance (e.g. the gradual increase in the wet acid deposition they have been receiving). Yet these streams appear to have resilient communities. This may be due to the characteristics of the organisms, which Townsend (1989) describes as being 'weedy'.

This study has shown that the patterns of persistence for the Ashdown Forest streams are repeatable and that pH is the variable of most importance. The UKAWMN sites also show some evidence of community persistence, although they experience very different and, in some respects, harsher environmental conditions. There are still four years of data collection to come for the UKAWMN stream sites (the survey was planned to cover a ten year period from 1988), and it would be interesting to reassess these sites again using a longer run of data. These communities may be impoverished but they are predictable.

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